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Acanthocephala of North American Mammals

HARLEY J. VAN CLEAVE

ILLINOIS BIOLOGICAL MONOGRAPHS: *Volume* XXIII, *Nos. 1-2*

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ACANTHOCEPHALA OF NORTH AMERICAN MAMMALS

Acanthocephala of North American Mammals

HARLEY J. VAN CLEAVE

ILLINOIS BIOLOGICAL MONOGRAPHS: *Volume* XXIII, *Nos. 1-2*

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URBANA, 1953

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FOREWORD

The completion of a series of monographs on the Acanthocephala of North America was the primary objective of Dr. H. J. Van Cleave during his last few active years. In December, 1950, while this work was in progress, he became seriously ill and was compelled to undergo major surgery. For sometime thereafter his health was considerably improved and he labored persistently to complete the task. As research professor he was able to devote his time to unfinished researches and to develop the broader generalizations such as taxonomic and host relationships, geographic distribution, etc., pertaining to this study.

A further interruption of his work came in July, 1952, when further surgery became necessary. Thereafter, completion of the task was even more painful and work was limited to brief sessions of a few hours' duration. The driving motive for this tenacity was the completion of the first of the series of contemplated monographs embodying a summary of the results of a lifetime of study of the Acanthocephala. The manuscript was finally completed in early December, 1952, and accepted for publication in the Illinois Biological Monographs. At the last, Professor Van Cleave had the satisfaction of knowing that the first of the monographs, *The Acanthocephala of North American Mammals*, was on the way to publication, completing the major portion of his last work.

The monograph as it now stands is a monumental review of much valuable research, and a wealth of first-hand information accumulated by Dr. Van Cleave through years of diligent study has thus become available and is shared with all other workers in the field.

After the manuscript had gone to press much further work remained to be done—proofreading, checking figures, compilation of the index, etc. The burden of this task was largely undertaken by Mrs. Jean Ross, research assistant to Dr. Van Cleave, and Dr. Francis J. Kruidenier, who was quite familiar with the proposed program. Thanks are due to both for their generous cooperation in the posthumous completion of this work.

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Head, Department of Zoology
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I. INTRODUCTION

The Acanthocephala or thorny-headed worms constitute a distinct phylum of the animal kingdom whose members invariably attain sexual maturity in the digestive tract of a vertebrate host. When undisturbed within the opened intestine of the host, the more or less elongated body is distinctly flattened (Van Cleave and Ross, 1945) but after removal to water or other medium for examination and after preservation the body becomes plumply cylindrical. This change in form accounts for the fact that for several generations helminthologists regarded the Acanthocephala as round worms. In life the body is slightly translucent or milky white although in some instances the worms pick up distinctive color from the materials in the lumen of the intestine. Attachment to the tissues of the host is accomplished chiefly through a highly modified, hook-covered anterior extremity known as the proboscis or primary organ of attachment. Other parts of the body (neck and trunk) may become secondarily modified (Van Cleave, 1952b) as accessory organs of attachment. There are no external appendages and highly specialized sense organs are entirely lacking. In fact, the body of both male and female adults is characteristically little more than a pouch for containing the reproductive organs of one sex and the modified structure mentioned above to guarantee firm attachment to the intestine of the vertebrate host. In the internal organization of the body not even the slightest remnant of specialized digestive organs is ever present at any stage of development.

The wall of the trunk is fairly simple in construction. It is bounded externally by a thin, non-cellular cuticula adjacent to which lies a relatively thick, fibrous hypoderm or subcuticula which comprises most of the body wall. Morphologically the subcuticula is composed of several distinct layers (Kaiser, 1913), the number varying in different groups of the phylum. The most conspicuous differentiation of the syncytial subcuticula consists of a series of inter-communicating spaces, called the lacunar system. Commonly this system has two main longitudinal vessels, either dorsal and ventral or lateral, but in some instances only the dorsal vessel is present. Smaller vessels, either as an irregular mesh-work or in fairly regular transverse series, communicate with the longitudinal trunks and ramify through all parts of the body wall. In species showing pseudo-segmentation (Text Fig. A) the regularly spaced lateral lacunae

and the body musculature provide the pattern for the constrictions which divide the trunk by repeated transverse folds. These folds are confined to the body wall and do not affect the arrangement of the internal organs as in animals with true segmentation. The lacunar spaces are never provided with epithelial linings. The subcuticula carries nuclei in pattern of arrangement and in numbers that are distinctive of the various orders (Van Cleave, 1928, 1948). The inner surface of the subcuticula is lined by the trunk musculature which consists of two syncytial fibrous layers, an external layer of circular fibers and an internal layer of longitudinal fibers, forming the lining of the pseudocoel (Hyman, 1951).

The pseudocoel holds all the truly internal organs, the most conspicuous of which are the reproductive organs, located chiefly in the posterior region of the body, enclosed in an axial ligament sac. In members of one order modified protonephridial organs (Meyer, 1932) are associated with the reproductive tract (Fig. 84) but in most species specialized excretory organs are wholly lacking. The reproductive system of the male consists of a pair of testes and specialized cement glands of varied cytological constitution (Van Cleave, 1949b) in the different classes of the phylum. Both the gonads and the cement glands discharge through a penis which is surrounded by a bell-shaped copulatory bursa. Except when functioning, the bursa lies in an introverted portion of the posterior extremity of the trunk. At copulation the extruded bursa is applied to the posterior tip of the body of a female where it is held securely in place by the secretions of the male cement glands. This material forms a hardened, resistant copulatory cap (Van Cleave, 1920) which is an internal cast of the bursa that remains attached to the genital area of the female for some time.

The reproductive system of the female is peculiar in that the ovary becomes fragmented into a large number of free-floating egg balls. Fertilization takes place as the ova leaves the egg balls. The fertilized eggs acquire the distinctive series of external membranes (Text Fig. F) which are not molded into shape by special apparatus such as is found in trematodes and cestodes. Once the ova resulting from early fragmentation of the ovary are all fertilized, the individual female is at the end of her reproductive cycle, since additional eggs cannot be produced. The fertilized eggs are retained within the body of the female until fully embryonated. The persistent portion of the female reproductive system consists primarily of a highly modified tube (Fig. 95) which at the genital orifice consists of a vagina closed by a heavily muscular sphincter. A uterus extends anteriorly from the vagina. In it three divisions are distinguishable. The posterior region is a saccular uterus the entrance to which is guarded anteriorly by a series of guard cells called the selective apparatus and from this a funnel-like uterine bell opens into the body

cavity or into one of the pair of ligament sacs holding the developing eggs. Immature eggs, which are directed into the uterine bell by peristaltic contractions of the bell, are by-passed through special openings in the walls of the selective apparatus and are thus returned to the body cavity or the ligament sac. Fully embryonated eggs are passed on down the uterus and are eliminated through the vaginal sphincter.

Within the anterior end of the body are found the muscular sac known as the proboscis receptacle, the lemnisci, and musculature for retracting the proboscis receptacle and neck. The proboscis receptacle furnishes some of the most reliable taxonomic characters. It is usually attached at the posterior end of the proboscis although in some genera it joins the inner surface of the proboscis wall considerable distance anteriorly. Muscles known as invertors of the proboscis are inserted on the inside of the anterior tip of the proboscis and extend through the length of the proboscis and its receptacle. At the posterior end of the receptacle, or in some instances through a cleft (Fig. 86) in the ventral wall of the receptacle, the invertor muscles leave the receptacle and pass into the body cavity. There they continue for some distance, one finding attachment on the dorsal wall of the trunk and the other on the ventral wall. Contraction of the anterior part of these longitudinal fibers introverts the tip of the proboscis while contraction of the posterior part of the same fibers withdraws the entire receptacle more deeply within the cavity of the body. A sheet of muscles attached to the neck causes the neck to be tucked in and folded around the base of the proboscis (Van Cleave and Bullock, 1950) when contracted. These neck retractors are rather intimately associated with the pair of distinctive long, tubular or flat, ribbon-shaped, or short, broadly flattened organs known as the lemnisci (Fig. 128). The latter are outgrowths from the subcuticula of the neck, extending backward into the body cavity.

The brain, or chief ganglion of the central nervous system, is a small mass of nervous tissue located within the cavity of the proboscis receptacle. Most of its delicate main trunks are very indistinct but usually two of them, the retinacula, have conspicuous muscle fibers associated with them and these pass through the wall of the receptacle to innervate the body wall. A small, inconspicuous genital ganglion is associated with the copulatory apparatus of the male, near the posterior extremity of the body.

In the foregoing brief summary, all of the more important morphological structures characteristic of the Acanthocephala are mentioned. Some of the features, such as the body divisions and the proboscis hooks, will be discussed in the section on Morphology.

All Acanthocephala are so completely dependent upon the parasitic mode of existence that there is no exception to the rule which states that

no member of this phylum ever exists in nature as a free living organism, even for a short time. The hard-shelled egg (Text Fig. F) never hatches (Text Fig. G) normally as an acanthor (Van Cleave, 1947b) until it is swallowed by a suitable arthropod which, so far as known, is always the essential first intermediate host. Within the arthropod the acanthor undergoes metamorphosis to a more advanced series of stages known as acanthellas (Text Figs. H and I), in which rudiments of the organs of the adult make their appearance. The juvenile worm, with all of its organs blocked out, becomes encysted as an infective larva or cystacanth (Text Fig. J), either in the arthropod or in some other intermediate host.

In the least complicated life cycle, the final vertebrate host invariably acquires its burden of larval Acanthocephala by eating infected arthropod hosts. The life cycle may be prolonged and complicated by the introduction of one or more additional intermediate hosts between the first intermediate and the definitive hosts. The second, and in some instances a third, intermediate host may be any suitable invertebrate or vertebrate in which the infective acanthocephalan larva (Fig. 108B) can become established in a visceral cyst (cystacanth). The newly acquired host must feed upon the earlier intermediate host and in turn must serve as a food element for a later intermediate host or for the definitive host. There is no means, other than through food chains, for the parasite to gain entrance into each succeeding host. Therefore the habitat and feeding habits of each species of vertebrate largely determine the susceptibility of that species to acanthocephalan infection and at the same time these factors control the intensity of the individual infection of any host.

The phylum is world wide in its geographical distribution but its genera and species are not of uniform distribution since certain species are practically cosmopolitan while other species and genera are rigidly confined to a limited area. This limitation is never the direct effect of the external physical environment on the parasite. The external physical surroundings may directly restrict the distribution of one or more of the essential hosts of the acanthocephalan. Physiological adaptation between the parasite and the host, whose body provides the environment of the worm, often furnishes obstacles to the worm becoming safely established in any animal other than its natural hosts. Although host specificity is fairly well established for some species of Acanthocephala, other species have relatively wide range of host tolerance, but never does the same species occur as normal adults in both cold-blooded and warm-blooded definitive hosts. In the few instances where this rule seems to be violated there is evidence that one of the hosts is the result of accidental infection and that the parasites are unable to reach full sexual maturity in it.

More species are encountered in fishes than in any other vertebrates

and these include a large proportion of the forms which are regarded as the most generalized. This statement is sometimes cited as basis for the belief that *Acanthocephala* were parasitic in fishes before the other vertebrate groups had their origin. Many of the highly specialized forms occur chiefly in birds and mammals but some of the more generalized families have genera or species that seem to have become secondarily established in birds and mammals. This might be explained by the fact that some birds and mammals have become closely associated, ecologically, with the lower vertebrates in the aquatic habitat.

The intensity of infection in individual hosts varies widely for different species of host and for different species of parasite. In many instances one or a few worms are encountered in the intestine of a host but some individuals have the favorable regions of the intestine completely filled with living worms. These differences are attributable chiefly to relative abundance of suitable intermediate hosts and to the food and feeding habits of the vertebrate definitive host. According to Burlingame and Chandler (1941:10) mechanical crowding in the host intestine does not determine the size of the individual worms, for in *Moniliformis* they observed that the largest females are found in the most densely populated areas of the rat intestine.

There are definite limits to the growth of all species of *Acanthocephala*, but in some species of host the individuals attain greater length than in others. The adult worms of the various species are extremely diverse in size, ranging from about 1 mm in some species from fishes to over 400 mm in length for some forms taken from mammals. With few exceptions most of the largest species are found as parasites of mammals but some of the mammalian forms (e.g., *Corynosoma*) are relatively small, although they occur in seals and whales.

It happens that the severity of individual infections and the number of species inhabiting the various groups of vertebrates follow the same general sequence, although this arrangement does not hold for all instances. Beginning with the largest number of species the vertebrate hosts would be placed in the following sequence: fishes, birds, mammals, amphibians, and reptiles.

In the evolution that has proceeded within the same family or subfamily to limit host relations, there is no sharp line of discrimination between the parasites of birds and those of mammals. Thus among the *Palaeacanthocephala* the subfamily *Polymorphinae* has the genera *Arhythmorhynchus*, *Polymorphus*, and *Filicollis* which normally occur exclusively in birds, the genus *Bolbosoma* which is found in mammals only, and the genus *Corynosoma* which has some species found normally in mammals only and others which are rigidly restricted to birds. Similarly within the *Archiacanthocephala* a corresponding diversification of host

relations is reflected within the family Gigantorhynchidae wherein the genus *Gigantorhynchus* is strictly a mammalian parasite while the species of *Mediorhynchus* invariably occur in birds.

For more than forty years the writer has been accumulating a study series of Acanthocephala from the Mammals of North America. In this effort a long list of colleagues and former students have been especially helpful in supplying material from regions not immediately accessible to the writer. The status of the taxonomy of this group of worms has been so unsatisfactory that the writer has refrained from publishing on these collections except in a very few instances where the evidences were especially clear. In the meantime several individual species have been recorded from this continent although no comprehensive treatment has as yet appeared. It has long been apparent that in North America the acanthocephalan fauna of land mammals has not undergone the extensive development of species and genera that it has in South America. Nor has the acanthocephalan fauna of mammals developed here the conspicuous evolutionary patterns that appear in the highly distinctive acanthocephalans of fresh water fishes and birds of North America.

II. ACKNOWLEDGMENTS

Through the years, while this investigation has been in progress, the writer has had free access to all of the government collections of the United States and many from Canada. Many of the important museums throughout the world and numerous scientists from other countries have graciously furnished specimens for comparison with the American collections of mammalian Acanthocephala. These loans have frequently contained type specimens and critically determined materials secured by expeditions to remote parts of the earth. Except for the hearty and generous cooperation of friends and colleagues, this study could not have gone beyond a local study with notes on a few isolated collections. Many individuals have continued through the years to send to the writer all of the specimens which they and their associates have encountered in field studies. The following list includes only those American colleagues who have aided materially in the accumulation of the study series. The study has extended over such a long period of time that more than a few of the contributors have died before this work was completed. To all of these friends the writer expresses a deep sense of gratitude for their cooperation.

American Collaborators.—J. E. Ackert, B. Babero, C. W. Bazuin, H. K. Buechner, Carlos Calero, T. W. M. Cameron, W. P. Canavan, A. C. Chandler, G. E. Clark, R. Combs, A. R. Cooper, C. W. Deslandes, W. E. De Turk, H. Douthitt, A. B. Erickson, H. E. Essex, F. B. Hadley, S. Hadwen, M. C. Hall, C. A. Hannum, A. Hassall, A. C. Hawbecker, C. M. Herman, A. G. Humes, B. F. Kaupp, A. L. Kelly, Harold Kirby, Iola Musefeldt Knight, Joanna Krogsdale, W. Henry Leigh, D. R. Lincicome, Betty Locker, J. E. Lynch, C. A. McLaughlin, Frank McMurry, H. W. Manter, C. W. Markus, Luis Mazzotte, M. C. Meyer, J. D. Mizelle, D. V. Moore, Sam Morris, W. M. Morton, J. F. Mueller, J. R. Olive, J. W. Parker, E. W. Price, John S. Rankin, B. H. Ransom, J. H. Sandground, V. B. Scheffer, E. L. Schiller, J. Teague Self, C. M. Senger, J. N. Shaw, C. W. Stiles, J. D. Tiner, B. V. Travis, H. L. Van Volkenberg, Henry B. Ward, R. A. Wardle, and R. B. Williams.

Foreign Collaborators.—The following is a list of individuals and museums that have provided significant materials of Acanthocephala from mammals of other parts of the world for comparison in the present study. Among these are the following individuals: J. E. Alicata (Hawaii), J. G.

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Special Aids.—A grant from the National Research Council became available in 1932 to provide aid in the preparation of whole mounts and of sections of the material then available for this study and for other programs of research on the Acanthocephala. Although numerous small collections were then available, so many problems arose in the course of the attempt at identification of the material that the results of the study were withheld until more extensive collections could be secured. This accounts for the belated acknowledgment and expression of appreciation for the grant from the National Research Council. For many years, in the continuation of this program, the Department of Zoology in the University of Illinois has furnished the writer with a research assistant, relieving him from the responsibilities of accessioning and preparing the collections for study.

The writer is particularly indebted to the research assistants who have served in this project. Of these, especial thanks are due to Mrs. Jean A. Ross who through a long period of cooperation has become highly skilled in preparing difficult materials and who has reclaimed many hundreds of microscopic mounts that had faded or become otherwise damaged. It is a pleasure to acknowledge her competent aid, not only as a technician but also as one capable of interpreting likenesses and differences between specimens and of understanding biological principles in their relations to taxonomy.

The distinctive, analytical line drawings illustrating this monograph were prepared by the scientific artists in the Department of Zoology, Katharine Hill Paul and, more recently, Charles A. McLaughlin, both of whom have been most graciously cooperative.

III. PREPARATION OF SPECIMENS FOR STUDY

Among the earliest students of Acanthocephala, and extending down to the present generation of helminthologists, there has been a very general feeling that uniformity in fundamental structures, tantamount to extreme monotony of form, exists throughout the members of this phylum. This impression, more than any other single item, is probably responsible for the slow early growth of taxonomy of the Acanthocephala above the level of species. Superficial examination easily confirms a degree of uniformity in general plan of construction which limited early specific diagnosis to the enumeration of a few morphological specifications most of which were confined to statements about relative or absolute size of the body and its constituent parts and differences in number of a few structures such as the proboscis hooks. Many of the early investigators assumed a high degree of host specificity.

As a relatively ancient group of worms adapted to obligatory parasitism through the entire life of every individual, all of the structures distinctive of free, independent life have been entirely eliminated. There are no external appendages, no specialized sensory structures, no specialized digestive organs. As an accompaniment of the stripping away of these morphological features, the body of an acanthocephalan has become extremely simplified. The elimination of so many of the anatomical features greatly reduces the number of avenues available for expressing significant differences. In fact, the body of an adult acanthocephalan is little more than a bag for housing the reproductive organs and one or more modifications of special structures for attachment of the worm to the wall of the host intestine. Reduction of essential specifications to a morphological formula this simple involves extended rationalization and generalization on the part of the observer. Only the untrained eye is directly impressed by the monotony of appearance in the various kinds of Acanthocephala. The skilled observer may ultimately reach the same conclusion but only after active elimination of earlier impressions of diversity.

The early studies of Kaiser and Hamann in the closing decade of the nineteenth century established the fact that many features of acanthocephalan structure find diverse expression when their finer details are considered. Their works further demonstrated that the impression of monotony results from superficial examination of structures which in

reality show many significant differences after histological details are analyzed. However, the recognition and interpretation of many of these features require special techniques of preparation which the novice is unwilling or unable to perform. The final basis for recognition of many of the well established genera is obtainable only from the study of serial sections or of carefully prepared, stained whole mounts. Often the full evidence is unavailable in either the living or ordinarily preserved specimens. Consequently the preparation of material for critical study is extremely important. This begins with the removal of the worms from the host, continues with proper killing and preservation of the specimens, and finally the mounting of stained individuals or preparation of serial sections.

Disappointing Collections.—To the student of taxonomy and morphology of parasitic worms there is nothing more disconcerting than inadequately prepared material. Workers on exploring expeditions and those on general faunal surveys often have no special training in preparation of parasitic worms for study. As a result Acanthocephala and other parasites are commonly dropped into preservative without previous treatment and attached worms are often torn from the host intestine, leaving the severed proboscides embedded in the tissues of the host. The most thoroughly unsatisfactory material is that which is recovered from entrails that have been dropped into formalin or other preservatives to be examined later. Much of the material so recovered has little value because of distortion of the body and the fact that the features essential for identification are obscured or lacking. It is often wholly impossible to make either generic or specific identification of material of this sort. Even though some individuals may be identifiable, the frequent occurrence of mixed infections of Acanthocephala in the same host individual precludes the possibility of assuming that other specimens, less favorably preserved, belong to the same species.

Removal of Worms.—Adult acanthocephalans are normally found only within the lumen of the intestine of a vertebrate host. If alive, the proboscis is usually embedded in the tissues of the intestinal wall. Unless removed with care the proboscis will be broken off and left in the intestinal wall, or its hooks, which are essential for identification, may be torn loose. A gentle pull often dislodges the proboscis but in some species the proboscis or other region of the body is swollen within the host tissue as an accessory attachment adaptation, so that removal by pulling is impossible. A pair of fine-pointed dissecting needles may be inserted in the crater-like opening in the host tissue, surrounding the proboscis. By careful manipulation of the needles the crater may be spread wide enough to free the proboscis of the worm.

For instances where entire worms cannot be pulled from the intes-

tine of the host, it is best to cut several small squares of the intestine, each holding an embedded proboscis. After these have been preserved, the host tissue may be dissected away before the worms are stained and prepared for microscopic study.

Preliminary Treatment.—When living acanthocephalans are removed from the host intestine and placed directly in killing solution the bodies very commonly become badly contracted and in many the proboscis becomes introverted. In this condition the proboscis and its hooks are not available for study. To avoid this condition, it is common procedure in this laboratory to place small living worms in tap water in a Petri dish or Syracuse watch glass. Large worms, such as the giant thorny-headed worm of the hog, should be handled in glass saucers or larger utensils which permit full extension of the body. The change in osmotic relations causes the body to become turgidly distended and in this condition the proboscis becomes fully extruded. For a time the specimens retain the ability to introvert the proboscis upon stimulation but ultimately the proboscis remains fully extended even when touched. The length of time required for the worms to reach this state of inaction depends on several factors such as size of the worm, thickness and permeability of the body wall, and physiological state of the individual. Small, delicate worms may be ready for fixation in less than an hour while large ones may require several hours or even overnight. Occasional testing by probing with a toothpick or forceps reveals when the worms no longer respond and are therefore ready for killing in the relaxed condition.

Killing and Preservation.—Any good histological killing reagent is suitable for use on Acanthocephala but it is well to avoid those which cause discoloration of the tissues or leave salts deposited in the tissues. Alcohol-formol-acetic (A.F.A.: 85 parts 85 per cent alcohol, 10 parts commercial formalin, 5 parts glacial acetic acid) is one of the most effective reagents. Various modifications of A.F.A. are recommended by different workers but the solution mentioned here has proved generally very satisfactory for Acanthocephala.

After the worms have become immobile (as directed in the foregoing section) the excess of water is poured or pipetted from the dish, leaving only a thin film of water covering the specimens. The killing fluid, heated until vapor begins to rise, is poured over the worms. If previous treatment has been satisfactorily carried on, the specimen should not contract but should die in fully extended condition with the proboscis fully extruded and the body usually with both extremities curved slightly toward the ventral surface.

Tissues of small worms are usually properly fixed in less than an hour but exposure to A.F.A. for several hours or even days does not impair

the value of the specimens and ensures complete histological fixation of large specimens.

From A.F.A. the killed worms may be transferred to either 70 per cent or 85 per cent alcohol for permanent preservation or to await further treatment. If any other killing agent is used, care must be taken to remove any residues or any discoloration left in the tissues.

Bleaching.—Specimens that have been preserved for a long time are often darkly discolored, especially by tannic acid from corks. Such discoloration impairs the brightness of histological stains. When the preserved specimens have been run down the alcohol grades to water they may be bleached by mixing nascent chlorine with distilled water containing the worms. A very small amount of a commercial bleaching agent, such as Clorox, in water will perform the same action. In either case the bleaching process is hastened if the vial containing the worms is exposed to sunlight. Care must be taken to remove all traces of the bleaching agent by frequent washing in distilled water before attempting to stain the tissues.

Restoration of Shrivelled Specimens.—Specimens that have become shrivelled or hardened by drying or by improper preservation often may be restored to more nearly normal condition and appearance by treating with a warmed 0.5 per cent solution of trisodium phosphate in distilled water (Van Cleave and Ross, 1947). Prior to this treatment, alcoholic specimens should be passed down the alcohol grades to water, but completely dried worms may be placed directly in the relaxing solution. While undergoing this treatment, specimens should be kept under close observation since they may disintegrate if left too long or in too strong a solution. As soon as the worms become plump and pliable and are slightly translucent they should be transferred to distilled water to check the action of the detergent.

Before staining or other procedure is undertaken, all of the trisodium phosphate must be removed by repeated changes of the distilled water. If the worms are to be held for some time before preparation for mounting, they should be carried through the alcohol grades to 70 or 85 per cent alcohol for storage.

Staining.—Before proceeding with preparation of whole mounts, the specimens should be examined under a dissecting binocular. If fragments of host tissue, mucus, or fibers adhere to the proboscis they should be removed by the use of very fine needles before the worms are placed in stain. In this cleaning process, care must be taken to avoid damaging the proboscis or breaking off the hooks.

For best results, specimens should be slightly overstained and then destained to proper intensity of color. Many different histological stains are suitable for use on Acanthocephala but Borax Carmine, Acid Car-

mine, and Combination Hematoxylin are among those best suited for differentiating both superficial and deeper internal structures. The first two are standard biological stains. The Combination Hematoxylin is prepared by adding 1 cc each of Delafield's Hematoxylin and Ehrlich's Hematoxylin to 100 cc of distilled water in which 6 grams of potassium alum have previously been dissolved. This has the special value of but rarely overstaining.

For the Combination Hematoxylin, staining overnight is usually desirable while for the Carmine stains, especially Acid Carmine following treatment with trisodium phosphate, most of the specimens are sufficiently stained in less than an hour. Specimens may be taken into Borax Carmine from 70 per cent alcohol, into Acid Carmine from 85 per cent alcohol, and into the Combination Hematoxylin from distilled water. Occasionally an individual lot of worms may stain very unevenly or the color may be murky. In this laboratory it has become the practice to destain entirely such specimens and then to try a different stain.

Destaining.—Since both of the carmine stains are alcoholic, the worms may be transferred to 70 per cent alcohol for washing and destaining. From the combination stain the specimens should be washed thoroughly in distilled water and then passed through 35 and 50 per cent alcohol before reaching the 70 per cent alcohol where destaining is to be accomplished. A weak acid is best for differentiating the stain. Two to four drops of commercial hydrochloric acid in 100 cc of 70 per cent alcohol may require several hours to two days for destaining. The acid alcohol should be changed frequently and allowed to act until stain no longer leaches out of the tissues and the worms become slightly translucent. Thorough washing in 70 per cent alcohol will remove the acid and check the further destaining.

If the specimens to be mounted are relatively small and practically straight they may be carried along immediately for mounting but if they are very thick or long, or crooked, they require special treatment and handling.

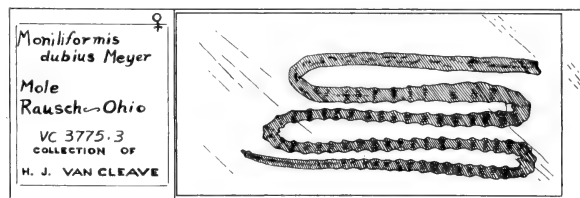
Arranging for Mounting.—Very thick worms which are not too long to be accommodated under a cover glass may be compressed slightly between two microscope slides. A strip of cardboard, of sufficient thickness to avoid too much compression, should be inserted at each end of the slide. Keep the specimen on a slide flooded with alcohol, preferably flat in a Petri dish. When the props are in place another slide is put flat on top of the worm and several loops of cotton thread are wound snugly around the slides, while applying some pressure against the faces of the slides with thumb and finger. When the ends of the thread are tied, the compressed worm between the two slides may be handled in Coplin or other stoppered jars for dehydrating. After reaching absolute alcohol,

the thread may be removed and the flattened worms will retain their shape off the slide if handled carefully to prevent undue bending or breaking.

Worms that are too long to mount under a cover glass must be given special attention. Either before staining or after destaining they may be oriented on a slide (Text Fig. A). To do this, the specimens should be somewhat softened in trisodium phosphate (0.5 per cent solution in distilled water). Lay a clean slide flat in a Petri dish and flood it with water. Along one edge of the top surface of the slide, place a narrow strip of cardboard or of thin wood. Stretch one end of the worm along the inner edge of this strip and then, judging the length of the cover glass to be used for the mount, place another strip in contact with the free edge of the worm. The remainder of the body can then be bent rather sharply around the end of the second strip. By repeating this process the worm is finally in a series of straight folds between the parting strips. Then a second slide is placed on top of the worm, the two slides are wound with thread as directed in the foregoing paragraph and in this condition the preparation is transferred successively to the series of jars for dehydrating.

Partial Dissection.—Some investigators have advocated cutting off the proboscis and mounting it separately. Others have followed the practice of cutting a radial section out of a large proboscis in order to secure information on the number and arrangement of the hooks. In both of these instances the result is mutilation that can easily lead to confusion in the interpretation of the severed parts. In so far as possible it is desirable to keep all parts of each individual together and thus avoid the confusion that may result from incorrect association of severed parts from two or more different individuals. There are some instances in helminthology where a confusion of records has resulted in parts of two different species or even different genera being considered as portions of the same individual. When such mismated parts become recognized as type of a new species or of a new genus the confusion is extremely unfortunate.

Even in fairly large worms the reproductive organs of the male may



TEXT FIG. A. Drawing of a permanent mount of a large acanthocephalan, showing details of labeling and method of orienting entire specimen.

be studied satisfactorily in stained whole mounts which may be made to accommodate themselves to the size of the cover glass as discussed in the foregoing section. In gravid females the body is often so filled with developing eggs and embryos that all internal organs are obscured. For large specimens in this condition, instead of cutting the worms into short segments to free the materials, it is much better to slit open the body wall. By shaking or by forcing water into the cavity with a medicine dropper many of the eggs may be removed before a permanent mount is made of the specimen.

Some species, as in the genus *Bolbosoma*, have an enlarged anterior trunk bulb which is so greatly inflated that compression between slides causes the tissues of the bulb to spread out over the neck and proboscis, obscuring these structures. For such specimens it has been found that two parallel longitudinal cuts through the swollen bulb removes the lateral surfaces of the bulb, leaving the proboscis and neck in their normal relation to the median slice of the bulb in a slice just a little thicker than the diameter of the proboscis. After staining and clearing the removed slices may be mounted, outer surface uppermost, on the same slide with the median slice, making the trunk spines available for study in surface view.

Dehydrating and Clearing.—The usual steps of 35, 50, 70, 85, 95 per cent and absolute alcohol are satisfactory for dehydration, allowing about an hour in each grade. In the steps from absolute alcohol onward every precaution should be used to avoid the specimens or the liquids coming into contact with the air. This can be accomplished by keeping the specimens and reagents in stoppered vials. If it is necessary to handle an individual specimen, it may be picked up on the tip of a sharply pointed, folded piece of paper which will hold some of the fluid around the worm and prevent air from drying the surface of the specimen.

To replace the alcohol, benzene is superior to xylene in this work because it does not harden the tissues. It is desirable to transfer the specimens from absolute alcohol to a mixture of equal parts of absolute and benzene. After about an hour the mixture may be replaced by benzene.

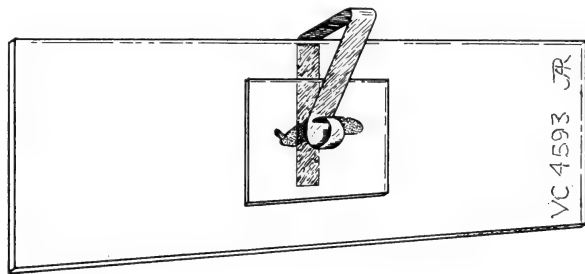
Mounting.—For permanent stained mounts, clarite, permatite, damar, balsam or any of the well established media soluble in benzene or xylene are satisfactory but here, especially, direct exposure of the surfaces of the worm to the air must be avoided or the mounts will turn opaque. Thin slivers of glass slide or cover glass, suited to the thickness of the worms, should be used to prop the cover glass, keeping it from tilting to one side. As the medium retracts from the edges of the cover glass while in the drying oven, it should be replaced with new mounting medium so that the entire area between slide and cover glass is filled. When the slide is thoroughly dry, a knife blade or other metal instrument, heated

to red heat, may be run around the edge of the cover glass. This effectively seals the edges and avoids further retreat of the medium from the edge of the sealed margins. Excess medium may then be removed from the surface of the slide and cover glass by scraping with a scalpel or a safety razor blade. After wiping the slide and cover glass with a clean cloth moistened with benzene or xylene to remove the powdered mounting medium, the mount is ready for study.

Spring Clips for Cover Glass.—In many laboratories it has been the practice to use vials containing lead shot or other small weights to apply enough pressure on the cover glass of fresh permanent mounts to avoid tilting of the cover glass while the mounting medium is drying. In this laboratory a much more satisfactory method for accomplishing this is the use of one or more small clips made from watch main springs (Text Fig. B). These apply uniform pressure and they are not subject to accidental displacement. The slide with one or more of these clips attached may be moved freely and even placed on the stage of the compound microscope for examination under low power.

Sectioning.—For serial sections no special directions are needed since the procedures of dehydration, clearing, embedding in paraffin, and cutting are identical with general practice in microscopic technic. If the worms intended for sectioning are treated with trisodium phosphate while still in water (after fixation of the tissues), the various liquids seem to diffuse more readily through the body wall than with material not so treated, ensuring complete infiltration of the paraffin.

Accessioning.—Too strong emphasis cannot be placed upon the necessity for keeping accurate records for each lot of material. The writer has found an extremely simple consecutive numerical system highly satisfactory. In a permanent accession book each lot of material is assigned a serial number. Full data as to host, locality, collector, date, number of specimens, method of killing and preservation, and all other pertinent



TEXT FIG. B. Drawing of a permanent mount of an acanthocephalan to show especially the spring clip designed to hold the cover glass in position while the mounting medium dries. The accession number of the material and the initials of the technician are etched on one end of each slide with a diamond pencil.

information are entered in the accession book beside the serial number. Thereafter the single number is all that is needed for infallible recognition of the material. Throughout all the procedures of preparation, that number on a slip of bond paper is carried inseparably with the specimens, not on the cover of the dish but in the fluid along with the specimens. When the final permanent mounts are prepared, the accession number is etched with a diamond marking pencil on the end of each glass slide (Text Fig. B) where it remains a part of the permanent record. Gummed labels bearing accession number and other data may become lost but through the number etched on the slide the full information is always available from the detailed record in the accession book. For recognition of individuals within any lot of material, the slides bearing each accession number are numbered serially as a decimal expression following the whole accession number.

Thus the record in the Van Cleave accession book shows that VC 4353 represents a single collection of specimens from "*Phoca hispida* #1, collected by R. Rausch, Point Barrow, Alaska, April 19, 1949. 7 slides." In the slide collection these are labelled VC 4353.1 to VC 4353.7. If the last of these is sectioned and placed on several slides, the sequence of the slides is indicated as VC 4353.7A, VC 4353.7B, etc. Until the permanent label giving full information as above is prepared, the serial number is all that is required for immediate recognition of any individual specimen.

IV. MORPHOLOGY

In the morphological and taxonomic descriptions of Acanthocephala there have been numerous inconsistencies in the methods of describing species and other taxonomic categories. Among many of the more prominent recent investigators, these inconsistencies have given way to a fairly uniform method of treatment of morphological features and standardization of measurements. However, to avoid possible misunderstanding, the following explanations seem essential.

Sex.—In all Acanthocephala each of the sexes is represented separately. It is almost invariably true that males in this phylum are smaller than females of the same species and age. In some few instances the bodies of the two sexes may be distinguished on size and form without examination of the internal reproductive organs. Basically the young of the two sexes are produced in essentially equal numbers but older infections of the definitive host commonly show a preponderance of females. This is due to the fact that males are expelled from the intestine of the definitive host after the task of fertilizing the females is completed. Thus it is not uncommon for an infection of long standing to consist largely or even exclusively of females. Since these carry developing embryos in their bodies, it is safe to assume that males were originally present in the same host individuals. The only alternative possibility for explaining the presence of the developing embryos would be that of parthenogenetic development of the females or a protandrous hermaphroditism. Both of these possibilities are refuted by all experimental and cytological evidences.

Since the two sexes often differ in fundamental structural features, which are not restricted to the sexual organs themselves, it often becomes necessary to offer a separate description for each sex, citing different limits of variability in measurements and appearance of distinctive structures as well as describing the morphological features characteristic of each sex.

Body Divisions.—Regardless of specializations of the various regions of the body in the various genera of Acanthocephala, the body in all members of this phylum is regarded as consisting of three morphological units or subdivisions—the proboscis, neck, and trunk (Van Cleave, 1952b). While these have been variously defined and interpreted in the

past, recent investigators have been in fair agreement as to the external boundaries of the respective regions.

The proboscis, the primary organ for attachment of the adult worm to the wall of the intestine of its vertebrate definitive host, is the anterior-most division of the body (Van Cleave and Bullock, 1950). In some instances it stands parallel with the main axis of the body but more often it is inclined, either slightly or sharply toward the ventral surface. Invariably the proboscis is provided with some sort of sharp pointed hooks although the size, number, and form of these vary widely. The proboscis is capable of introversion within an internal sac termed the receptacle of the proboscis. When in this position all of the hooks are withdrawn into the interior of the front part of the body with the tips of all hooks directed anteriorly in the central cavity formed by the introversion of the proboscis. As the proboscis becomes shot out from this position, the tips of the hooks engage in host tissue with which they come into contact and tear their way into that tissue with the tips of all the hooks turning posteriorly as they reach their functional position on the external surface of the proboscis. Because of its recurved point, each hook grapples tenaciously into the host tissues to secure the worm against the movement of food in the intestine which would tend to dislodge the parasite.

Regardless of its form, size, or adaptive modifications, the length of the proboscis is considered as the straight line distance between the free anterior extremity and the base of the thorn of the basalmost series of hooks. Measurements of the diameter of the proboscis do not include the thorns of the hooks which extend beyond the proboscis wall. In globular proboscides, a single diameter is all that is usually given and the same is true for those which are essentially cylindrical in form. Often the maximum diameter, with a statement as to its position, must be supplemented by diameters of other regions of the proboscis, depending on the shape of the organ.

The neck lies immediately posterior to the proboscis and serves as transition from proboscis to trunk. Its shape and extent are extremely variable but its limits are constant morphological features. The anterior boundary of the neck is the level of the posterior edge of the basal proboscis hooks while posteriorly it is marked by an inflected cuticular wall or collar which separates the wall of the neck from that of the trunk. Internally, this level is recognized by the fact that the lemnisci are inserted at the posterior extremity of the neck and from that level project into the trunk cavity. Contrary to the statements seen frequently in the literature, the neck is invariably devoid of cuticular spines or hooks. This error is due to the fact that some investigators have regarded as a neck the spiny posterior region of the proboscis in forms like *Gi-*

gantorhynchus. It is often desirable to give specifications of the diameters of the neck, especially in regions where there is either inflation or constriction.

In much of the older literature, measurements of the proboscis included either all or a part of the neck because of a general lack of appreciation of the morphological distinction between the two regions. In recognition of the fact that the neck is so closely related to the proboscis morphologically and functionally, Rauther (1930) proposed the term *praesoma* to include the neck and proboscis of all Acanthocephala. That term has become widely accepted in the literature since that time.

The trunk of an acanthocephalan comprises all that part of the body posterior to the cuticular fold or collar which marks the posterior boundary of the neck. This region contains all of the genital organs in both sexes and usually constitutes by far the greater part of the entire body of the worm. In gravid females it becomes turgidly filled with developing eggs held either in the trunk cavity or in special ligament sacs which come to occupy the entire trunk cavity.

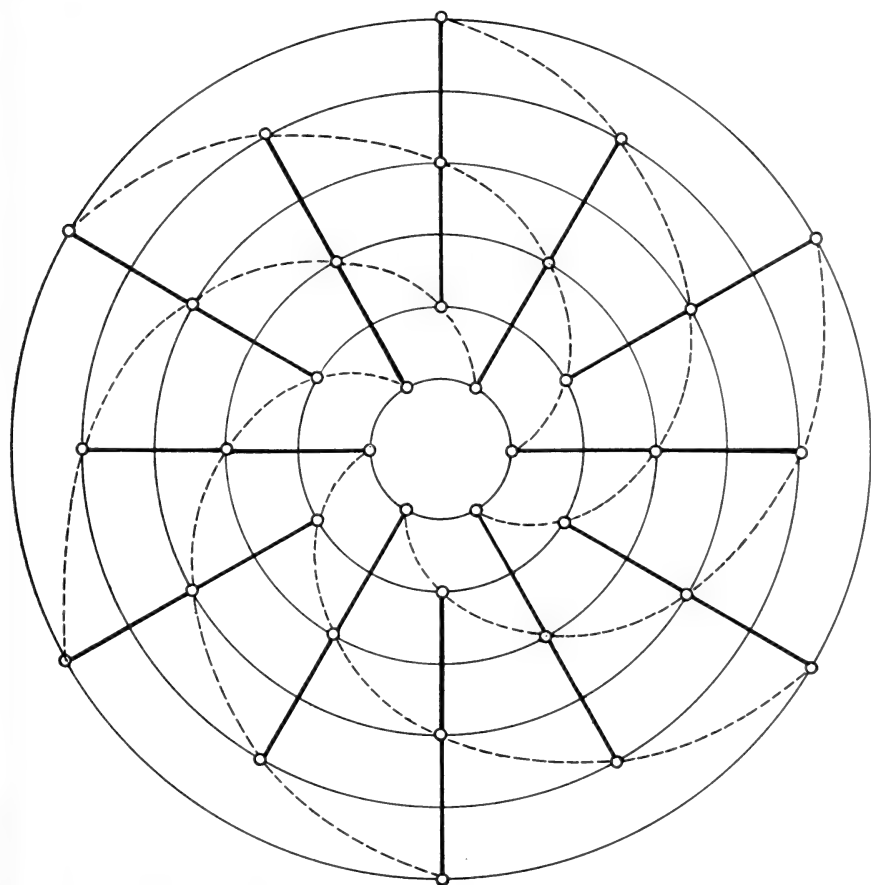
Proboscis Hooks.—Among features of the greatest value in taxonomy of all the Acanthocephala are the details of form, number, arrangement, and sizes of the proboscis hooks. Very commonly the hooks are arranged in quincunxial order so that longitudinal, cross, and diagonal rows are recognizable in the pattern of their disposal on the proboscis surface. However, size and density of the proboscis and crowding of the hooks on the edges of the rounded surfaces make the task of counting difficult. Often descriptions cite the number of longitudinal rows and the number of hooks in each. However, in some instances the arrangement does not follow a distinct pattern and especially in some of the Archiacanthocephala the formula is most readily expressed as spiral rows. Text Fig. C illustrates how the same pattern may be resolved into longitudinal, cross, and diagonal rows at will of the observer.

Except in most of the Eoacanthocephala and some of the Archiacanthocephala, there is considerable individual variability in the number and disposal of the hooks on the proboscis of individuals of the same species. Many of the early writers were not aware of this fact or ignored it and in consequence gave only a single fixed hook formula for each species. In most instances a range in number of hooks must be stated to convey a proper concept of the proboscis hooks. Wherever possible it seems desirable to express the formula in number of longitudinal rows and number of hooks in each row. Failure to specify whether longitudinal, cross, or zig-zag rows were considered has led to much misunderstanding of the early descriptions for many species of Acanthocephala.

In many instances, the hooks on the anterior and posterior regions of the proboscis have entirely different shape and size and often the smaller

hooks of the basal region possess no broadened root plates. It is likewise true that for many species the hooks shows progressive diminution in length posteriorly and anteriorly. In every case it is important that differences in form and size of the hooks be specified in descriptions. Some of the most recent investigators have failed to do this to the end that specific comparisons of otherwise sound descriptions are impossible.

In taking measurements of hooks, it is standard practice to measure the straight line connecting the free point of the thorn with the point where the thorn joins the root. Such measurements, to have value for comparison, must be confined to hooks in full lateral view in order to avoid the effect of foreshortening.



TEXT FIG. C. Diagram of an archiacanthocephalan proboscis, polar view, to show how hooks in quincunxial arrangement may be variously interpreted as to pattern. Heavy radial lines indicate twelve longitudinal rows of three hooks each; light circular lines pass through six circular rows of six hooks each; the spiral broken lines indicate six diagonal rows of six hooks each.

V. GENERAL TAXONOMIC SECTION

Earliest Taxonomy.—In the investigations of mammalian Acanthocephala before 1892, practically all of the species were ascribed to the genus *Echinorhynchus*. The chief exceptions were instances in which the earliest writers failed to recognize the Acanthocephala as an independent group of parasitic worms and consequently classified them under the name of some one of the more widely known group of worms. Thus Pallas (1766, 1781) referred to the giant thorny-headed worm of the hog as *Taenia hirudinacea* and *Taenia haeruca*, in part. In a very real sense this erroneous assignment of an acanthocephalan to the Cestoda is a commentary on his powers of observation. He was doubtless familiar with the living worms as they lie in the host intestine because they are then distinctly flattened like a tapeworm and do not at all resemble the *Ascaris* which commonly occurs along with them in the same host. Had Pallas observed them only in their turgidly preserved state, or after a helper had removed them to water for examination, he might have made the same mistake that many later observers made when they regarded them as round worms. After this widely dispersed species had finally been recognized as an acanthocephalan, the varied specific names under which it became known were regularly attributed to the genus *Echinorhynchus* as *E. gigas* or *E. hirudinaceus*. The historical development of nomenclature from these early names to the present-day acceptance of *Macracanthorhynchus hirudinaceus* (Pallas) is long and complicated, yet it is representative of the growth of nomenclature for mammalian Acanthocephala.

In 1892, Otto Hamann made the first critical analysis of taxonomic characters in the Acanthocephala at the level above species. At that time he recognized three families, each with a single genus. The only one of these groups distinctive of mammals is the family Gigantorhynchidae, based on the genus *Gigantorhynchus*, in which he placed the species *Echinorhynchus echinodiscus* Diesing. Since that date, the species of Acanthocephala from mammalian hosts have undergone intricate shifting and reassignment to various genera and families and as a further step in the construction of a comprehensive system of classification the families have been grouped into larger categories of orders and classes.

Rapid Expansion.—In the period from 1913 to 1926, Lauro Travassos published voluminously on his concept of the Gigantorhynchidae using

as the chief basis of his investigations the materials which he and earlier workers encountered in the distinctive mammalian fauna of Brazil. It is extremely unfortunate that some of the most important of Travassos' contributions were in publications which were apparently never received in any North American library and did not seem to be available to European investigators for verification of dates on which new names for taxonomic concepts were published. All of the writer's efforts to secure copies or photostats of some of these critical publications have failed. Furthermore, it is evident that especially early in his career Travassos followed the practice of citing the date on which a new name or description was presented on a scientific program, regardless of the date of its actual publication. The confusion which grew out this practice has been slightly alleviated by the publication (Lent and Freitas, 1938) in the *Travassos Jubilee Volume* of an apparently carefully edited list of his scientific publications in which the dates for many of the papers were changed from those on the periodicals or on the reprints. Many of these dates are also different from those cited in earlier, privately printed bibliographies of the publications of Travassos. In the present contribution frequent reference will be made to specific points in the determination of dates for the various names proposed in the publications of Travassos. For fuller elucidation of the validity of dates for names of Acanthocephala proposed by Travassos, the reader is referred to an article (Van Cleave, 1952a) which attempts to give a critical analysis of all acanthocephalan names proposed by that author.

The nomenclature of Travassos for the families and genera of Acanthocephala occurring in land mammals has been very generally accepted, although some minor modifications were introduced chiefly by individuals new to the field of acanthocephalan taxonomy and unfamiliar with the group as a whole. This wide acceptance extended down to 1931 when Anton Meyer (1931a) introduced a thoroughgoing revision of the taxonomy in anticipation of its adoption in his volume on the Acanthocephala in Bronn's *Tierreichs* (1932-33).

Reorganization.—In that monograph, Meyer undertook a complete reorganization of the classification of the Acanthocephala, accepting the proposals of some earlier workers and rejecting others in an attempt toward bringing the entire group into a completely integrated series of categories.

With the rapid expansion of morphological information that had accumulated since the closing decade of the nineteenth century, it became increasingly clear that the taxonomy of the Acanthocephala had grown not as a unit but rather as a series of independent categories. In a number of areas the taxonomy had progressed successively from the lowest level of specific recognition to one in which generic groupings of the

species had become well established. As still a further step, some of the genera had become widely recognized as basis for clearly defined families, but much of the taxonomic system had been sketched in only as a tentative framework with many species left dangling under the old all-inclusive generic designation of "*Echinorhynchus*, *sensu lato*." The time had apparently arrived when the thorny-headed worms were in need of a comprehensive revision and completion of the tentative and often conflicting classifications that had been advanced.

Classes and Orders of the Phylum Acanthocephala.—Meyer (1931a) proposed the names Palaeacanthocephala and Archiacanthocephala for two coordinate groups, which he regarded as orders, to include all the known Acanthocephala. Van Cleave (1936) showed that an apparent belief in a fundamental dichotomy in taxonomy had led Meyer to make an unfortunate alignment of families and genera to support his concept of only two major subdivisions of this phylum. This resulted in the inclusion within each of Meyer's major groups of a series of genera morphologically and ecologically incompatible with the distinctive families and genera on which the concepts rested.

As early as 1892, Hamann had clearly outlined the distinctive morphological features available for complete separation of the groups which Meyer had forced into his inharmonious assemblages. To correct this error, a third major group, the Eoacanthocephala, was proposed by Van Cleave (1936) as coordinate with the Palaeacanthocephala and Archiacanthocephala. Later (1948) Van Cleave recognized that the Palaeacanthocephala and Archiacanthocephala have certain fundamental features in common. This led to their being grouped together as a class, Metacanthocephala, under which the terms proposed by Meyer were retained as orders. At the same time, the order Eoacanthocephala was elevated to the status of a class, coordinate with the Metacanthocephala, and the groups Gyraacanthocephala and Neoacanthocephala which were originally proposed as suborders were elevated to full ordinal standing.

Thus, as the major classification of the thorny-headed worms stands at present, the phylum Acanthocephala comprises two classes, the Metacanthocephala and the Eoacanthocephala. The former of these, which includes all species normally reaching maturity in mammals of North America, is made up of two orders, the Palaeacanthocephala of Meyer and the Archiacanthocephala of Meyer, both as emended by Van Cleave (1936). For the sake of ready comparisons and contrasts, some of the more important features of the classes and orders are presented in Table I.

In their host relations, all groups of vertebrates are included among the definitive hosts of Metacanthocephala while cold blooded vertebrates

TABLE I. Tabular analysis of characters available for recognition of classes and orders of Acanthocephala (after Van Cleave, 1948).

Feature	Class Metacanthocephala			Class Eoacanthocephala	
	Order Palae- acanthocephala	Order Archi- acanthocephala	Order Gyracan- thocephala	Order Neoacan- thocephala	
Body size	Small to large	Mostly large	Small	Small	
Habitat of hosts	Aquatic	Terrestrial	Aquatic	Aquatic	
Longitudinal vessels of lacunar system	Generally lateral	Dorsal and ventral or dorsal	Dorsal and ventral	Dorsal and ventral	
Cement glands of male	Multiple, 6 or less	Multiple, usually 8	Syncytial	Syncytial	
Trunk spines	Present or wanting	Wanting	Present	Wanting	
Number subcuticular nuclei	Numerous amitotic fragments or few highly branched	Few highly modified and elongate	Very few giant nuclei	Very few giant nuclei	
Proboscis hooks	Radially arranged, ventral often larger than dorsal	Spirally arranged, ventral not larger than dorsal	Radially arranged, symmetrical	Radially arranged, symmetrical	
Proboscis receptacle	Closed muscular sac, 2 circular muscle layers	Ventral cleft, except in Moniliformis, one circular muscle layer	Closed sac, one circular muscle layer	Closed sac, one circular muscle layer	
Ligament sacs	Ruptured	Persistent, dorsal and ventral	Dorsal and ventral	Dorsal and ventral	
Nephridia	Lacking	Present or lacking	Lacking	Lacking	
Embryonic membranes	Thin	Heavy, sculptured	Thin	Thin	

alone, and almost exclusively fishes, serve as definitive hosts for the Eoacanthocephala.

Although there are many features which in combination usually are available for distinguishing between the classes Metacanthocephala and Eoacanthocephala, the single infallible distinction lies in the fact that the cement glands of the males of Metacanthocephala are invariably multiple while those of the Eoacanthocephala are just as regularly a single syncytial gland with a single cement reservoir which is lacking in all Metacanthocephala (Van Cleave, 1949b).

The class Metacanthocephala contains all the Acanthocephala which are normal intestinal parasites living in the intestine of mammals of North America. Although a few instances have been encountered wherein a small number of representatives of the class Eoacanthocephala have been taken from the digestive tract of a mammal, these are invariably accidental infections, unimportant in the biology of either the parasite or the host since there is no evidence that the Eoacanthocephala can ever develop to maturity in a mammal.

Biologically, it seems significant that all of the Palaeacanthocephala living normally in mammals of North America are found in hosts which live in or near the water, from which they secure at least a portion of their food. Conversely, all of the Acanthocephala of land mammals of this continent which are strictly associated with the terrestrial habitat fall within the order Archiacanthocephala.

Order Palaeacanthocephala.—All of the Acanthocephala occurring as adults in the intestine of aquatic mammals of North America belong to the order Palaeacanthocephala. Only two genera of this order, *Corynosoma* and *Bolbosoma*, occur in mammals. Both of these are included within the family Polymorphidae and the subfamily Polymorphinae. All representatives of these two genera are primarily adapted to the aquatic environment although in some instances the host-parasite relationship has become secondarily established in birds and mammals which are not strictly aquatic although they have definite habitat relationships which bring them into contact with the aquatic habitat. The species of these two genera which are normal parasites of mammals invariably seem to utilize fishes as a second intermediate host through which infection is carried from the arthropod first intermediate host to the mammalian definitive host by way of food chains.

Since no other families or subfamilies of Palaeacanthocephala occur in mammals of North America, the single subfamily Polymorphinae will be discussed here.

Polymorphinae Defined.—The Polymorphinae comprise all the Palaeacanthocephala with trunk spines that are parasitic as adults in birds and mammals. The subcuticular nuclei of the trunk wall are amitotically

broken into a large number of small, scattered fragments. The multiple cement glands (two to eight) are either ovoidal or elongate tubular, each consisting of a cortical layer containing many small nuclear bodies and a central lumen for storage and transport of the cement. The proboscis receptacle invariably has two concentric muscular walls. In their life histories, all members of this subfamily are directly connected with the aquatic environment.

The genera *Corynosoma* and *Bolbosoma* will be diagnosed in another section where their respective species will come under consideration.

Order Archiacanthocephala.—In the early works of Travassos, the Gigantorhynchidae assumed the proportions approaching the direct equivalence of the Archiacanthocephala as constituted at the present time after Van Cleave (1936) emended Meyer's proposal by separating off the irreconcilable family Neoechinorhynchidae to a separate order. In the Meyer monograph (1932:26) the concept of the Gigantorhynchidae as formulated by Travassos was replaced by a series of five presumably distinct families; Apororhynchidae, Gigantorhynchidae, Oligacanthorhynchidae, Moniliformidae, and Pachysentidae. In the present publication, the family Pachysentidae is regarded as a direct synonym of Oligacanthorhynchidae. Neither the family Apororhynchidae nor the Gigantorhynchidae has any representative reaching maturity in North American mammals and hence will not be considered further in this publication.

Many of the species and genera at present included within the family Oligacanthorhynchidae were originally assigned to the Gigantorhynchidae by Travassos (1917, *et seq.*) who greatly expanded the original inclusion of that family as proposed by Hamann (1892).

Meyer (1931a) erroneously laid claim to authorship for the family Oligacanthorhynchidae and for the concept which it covers but in this proposal and recognition he was antedated six years by Southwell and Macfie (1925:152). Meyer (1931a) broadened the scope of the family Oligacanthorhynchidae by adding to it four more genera of which *Nephridiorhynchus*, *Nephridiacanthus*, and *Travassosia* were of his own creation and a fourth, *Hamanniella*, had been proposed earlier by Travassos. In the present monograph it is shown that *Travassosia* is a synonym of *Hamanniella*. Through his studies, Meyer greatly extended the morphological description of the family but these additions do not alter the fact that the name and the concept are both attributable to Southwell and Macfie. Those authors based their diagnosis chiefly upon differences in the proboscis and neck of Gigantorhynchidae and Oligacanthorhynchidae but, unfortunately, they were in grave error when they interpreted the elongated basal region of the proboscis in *Gigantorhynchus* as a thorn-bearing neck. Leading investigators in acanthoceph-

alan morphology have long recognized the fact that the neck is never supplied with spines or hooks and that it is a morphological and physiological entity readily distinguishable from the proboscis.

Objective or Subjective?—Along with the multiplication of number of genera and of families in the Archiacanthocephala, the difficulty of distinguishing between them became increasingly great. In his characterization of genera and families, Meyer placed emphasis upon relative size and form of the body and biological characters such as the group in which the hosts belong. The latter may have distinct value but when it is not supplemented by any morphological feature its use as a diagnostic character is of doubtful or at least limited validity. In some instances not a single feature was mentioned for separating two families or two genera. Many of the groups lacked clear cut features for recognition so that positive identification was difficult or impossible.

In attempting to solve this problem of identical concepts recognized under two different names, it has been found necessary to reduce the family Pachysentidae to synonymy with Oligacanthorhynchidae and also to regard one of the genera of the Oligacanthorhynchidae, *Travassosia*, as a direct synonym of *Hamanniella*.

Family Pachysentidae Invalidated.—For a number of years the present writer felt that this might be a subjective condition arising from the fact that criteria for the recognition of genera and families in the Archiacanthocephala are obviously different from conditions that maintain for the other orders. After an objective approach to the solution of the difficulty of recognizing genera and families, it became apparent that many of the features for differentiation are purely relative. In the other orders of Acanthocephala it has been customary to rely upon discreet differences which are at the same time qualitative and quantitative in nature. Consequently, when Meyer (1933:531) presented a key to the families and genera of Archiacanthocephala and in this key relied wholly upon relative characters, the writer felt that questioning the soundness of the distinctions was no longer attributable to subjective biases or personal limitations. In that same key, size and shape of the body and the intergrading conditions of the shells of the embryonated eggs are the only distinctions mentioned as available for separating the Oligacanthorhynchidae from the Pachysentidae. These are features which merit no value above that for distinguishing between species. Consequently it becomes necessary to recognize that the Pachysentidae are indistinguishable from the Oligacanthorhynchidae, and Oligacanthorhynchidae becomes the valid name for the family.

Family Oligacanthorhynchidae.—Acanthocephala of medium to large size, parasitic as adults in land mammals and birds. The life history is known for only a few of the species and these include some forms which

involve only two hosts, an arthropod as intermediate host and a bird or a mammal as definitive host. Commonly, in these simplest life cycles, the cystacanth is introduced into the intestine of the definitive host when that animal feeds upon infected beetles or soil-inhabiting beetle larvae and these in turn secure the larvae by feeding upon the eggs of the acanthocephalan. For a number of other species, a least three hosts are involved. In such instances a second intermediate host is interposed between the arthropod and the definitive host. An example of this modified life cycle is that in which a snake or amphibian devours infected arthropods and the cystacanths become encysted in the tissues of the new host to be passed on to the definitive host when a suitable bird or mammal feeds upon the transport host. The two species of the genus *Macracanthorhynchus* are the only North American representatives of the family for which the life cycle has been investigated. In both of these species only the arthropod is essential as an intermediate host.

Travassosia Invalidated.—Travassos (1917a) recognized a species of *Acanthocephala* which he encountered in a Brazilian armadillo as a distinct species of the genus *Hamanniella* under the name *H. carinii*. He had established the genus to which he assigned this species in 1915 to include a single species from a Brazilian opossum. Meyer (1932), using characters which had never before been generally recognized as having more than specific value, created a new genus, *Travassosia*, to receive *H. carinii* as type, differentiating the new genus largely on the proportions of the body (compare Figs. 85 and 91).

More recently a careful check, by the present writer, of the features used in diagnosis of that new genus reveals not a single valid point for distinguishing it from *Hamanniella*. Consequently in the present contribution *Travassosia* is reduced to direct synonymy with *Hamanniella*. This fact was not appreciated until after the present writer had described a new species from a North American armadillo under the name of *Travassosia tumida* but that species now must become *Hamanniella tumida* (Van Cleave, 1947a).

Diagnosis of Oligacanthorhynchidae.—External surface of trunk (Fig. 85) often with irregular transverse folds. Main longitudinal vessels of the lacunar system commonly dorsal and ventral. Proboscis globular or ovoid, armed with 6 or 7 spiral rows of from 5 to 8 hooks each. Each of the larger anterior hooks often has a single barb near the tip, formed by a straight beveling of the concave margin; the posterior end of the beveled point slightly overhangs the adjacent part of the shaft to form the barb. Roots of hooks well developed as either symmetrical or asymmetrical outgrowths. Receptacle of proboscis inserted either at the base or within the interior of the proboscis; its wall a relatively heavy internal layer of muscle with prominent cross fibers and a very thin outer layer of longi-

tudinal fibers. The thick, internal muscular layer, much thicker on the dorsal than on ventral surface, is interrupted by a prominent cleft on the ventral surface through which the proboscis inverter passes as the retractor of the receptacle. Brain near ventral cleft, inside the proboscis receptacle. Lemnisci cord-like or flattened, with a relatively small number of giant nuclei. Protonephridial organs associated with the genital tract. Male reproductive organs in or near the posterior half of the body cavity. Testes usually elongated; eight uninucleate cement glands, often arranged in pairs.

The family Oligacanthorhynchidae has the following genera known to occur in North American mammals: *Macracanthorhynchus*, *Hamanniella*, *Onciola*, *Pachysentis*, and *Echinopardalis*. These genera and their included species will be considered in another section of this work.

Family Moniliformidae.—The generic name *Moniliformis* was proposed by Travassos (1915b) to include as type *Echinorhynchus moniliformis* Bremser, 1811. By original assignment, the genus was allocated within the family Gigantorhynchidae where it remained until 1925 when Van Cleave called attention to the morphological details which exclude it from that family. At that time the name Moniliformidae was proposed and subsequently no other genus has been added to this family.

Diagnosis of Moniliformidae.—Trunk often with conspicuous pseudo-segmentation (Text Fig. A) which affects only the body wall. Proboscis nearly cylindrical, with numerous small, crescentic hooks (Fig. 121) in which there is no sharp separation of thorn and root. Proboscis receptacle a closed sac (Fig. 118) the outer muscular wall of which has groups of fibers running conspicuously in oblique direction. Lemnisci long, cylindrical. Eight cement glands of male uninucleate. Mammals, and especially rodents, are normal definitive hosts although other mammals have been reported as host for several of the species. A detailed analysis of the species assigned to the single genus *Moniliformis* will be presented in another section.

Family Gigantorhynchidae.—As indicated elsewhere in this section, the concept of the family Gigantorhynchidae was recognized by Hamann (1892) for the single genus *Gigantorhynchus* but that concept underwent rapid expansion, especially at the hands of Travassos who added a considerable number of genera. As a consequence, this family came to be recognized as the only one distinctive of land mammals. However, when Meyer (1931a) formulated his taxonomic system the family Gigantorhynchidae was left with presumably three genera, *Gigantorhynchus*, *Mediorhynchus*, and *Empodius*. The last of these is indubitably a direct synonym of *Mediorhynchus* and thus only two genera constitute the family Gigantorhynchidae as now constituted. Of these the genus *Gigantorhynchus* is one of the most rigidly limited of all

acanthocephalan genera both with regard to its geographical distribution and its host relations. In the literature it has been reported from three species of Edentata belonging to the suborder Xenarthra: *Tamandua tetradactyla* (the collared anteater), *Myrmecophaga jubata* (the giant anteater), and *Cyclopes didactyla* (the little anteater). *Gigantorhynchus echinodiscus* (Diesing) is widely distributed in these three hosts in Brazil and additional records from *Tamandua* are known for Panama and for the Island of Trinidad. It is highly probable that the host-parasite relationship is a very old one; for *Myrmecophaga* and *Tamandua* originated as genera in the Pleistocene and have not spread into North America.

In contrast, *Mediorhynchus*, the other genus of the Gigantorhynchidae is world-wide in the composite distribution of its numerous species and in each country uses a fairly long list of native birds as definitive hosts.

Since no species occurs in mammals of North America, the family Gigantorhynchidae will not be given further consideration in this work.

Family Apororhynchidae.—To complete the picture of the revamping of the original concept of the Gigantorhynchidae, still another family has been added and although this does not occur in mammals it will be mentioned here in order to show its relations to the older and the modern classifications. The genus *Apororhynchus* (= *Arhynchus*) of Shipley (1899a), was based on a single species from a bird of the Sandwich Islands. As originally described, several of the morphological details of this species were misinterpreted. As a consequence the genus was regarded as showing no direct relationship with other genera and was recognized as type of a new family to which the name Apororhynchidae (Shipley, 1899a) became attached. Meyer (1931a), on the basis of a single female specimen in the Berlin Museum, described a second species from a Brazilian bird, without adding materially to an understanding of the morphological and taxonomic relationships of the genus and family. The only comprehensive morphological treatment of a representative of this genus is the description of *Apororhynchus amphistomi*, from two species of North American warblers, by Byrd and Denton (1949) who had the advantage of studying living specimens as well as serial sections and whole mounts. Largely on the basis of a lack of a distinct proboscis receptacle, these writers claimed independent ordinal status for this genus. Although they cited the work of Thapar (1927) and that of Witenberg (1932) in their bibliography, they did not mention the fact that both of these workers had independently made the same proposal. It is the opinion of the present writer that many of the morphological features shown by *Apororhynchus* are fundamentally similar to

those of *Mediorhynchus*, and points of departure are in large measure simplifications of features present in that genus. Meyer (1931a) placed *Apororhynchus* in the *Archiacanthocephala* adjacent to the *Gigantorhynchidae*. Long before Meyer published his monograph this was the position to which the present writer assigned the genus *Apororhynchus*, and at times he has even doubted the validity of recognizing a separate family because of the close adherence of *Apororhynchus* to general morphology found in the genus *Mediorhynchus*. No widely recognized specialist in the taxonomy of the *Acanthocephala* has accepted separate class or ordinal status for *Apororhynchidae*. Since mammals are not known as hosts of *Apororhynchus*, that genus will not be discussed further here.

VI. CORRELATION OF HABITAT WITH TAXONOMY

Land versus Aquatic Forms.—Practically all of the Acanthocephala from land mammals belong to the order Archiacanthocephala as modified by Van Cleave (1936, 1948). This order seems to find its fullest expression in the mammals of South America and Africa where primitive mammals abound but the order does not occur in Australia, as will be discussed in another section. The parasites of aquatic mammals and of those which have some direct association with the aquatic habitat belong to the order of Palaeacanthocephala. Meyer has shown that these parasites have embryonic shells which do not require drying as do those of species directly associated with the terrestrial habitat. This order contains so many parasites of fishes and birds that it seems probable that mammals through association with the aquatic habitat have secondarily acquired parasites that were primarily adapted to lower vertebrates. Similarity of food habits and identical ecological surroundings of diverse aquatic animals would facilitate such a shift of host relations.

Habitats of Palaeacanthocephala.—The various species of the genus *Corynosoma*, in their normal definitive host relations, include hosts from both marine and fresh water habitats. In North America, *C. constrictum* and *C. anatarium* from ducks seem to be limited to the fresh water environment and similar conditions are known for one species, *C. mergi*, known to occur in water birds of Sweden and Alaska. Some individual species of *Corynosoma* are very widely distributed, especially in marine mammals, but the Arctic fauna is entirely distinct from that of the Antarctic. Furthermore, it seems probable that no species occurs on both sides of the equator. A few instances to the contrary reported in the literature are probably based upon erroneous specific determinations.

The genus *Bolbosoma* occurs normally in the marine habitat only, with cetaceans as the only natural definitive hosts. Probably because of the herculean task of autopsying a whale, records of *Bolbosoma* for most parts of the earth are very incomplete. The fish hosts are distinctively marine, although some may be taken in fresh water following migration from the sea.

Host Relations of Palaeacanthocephala.—While *Corynosoma* of the subfamily Polymorphinae includes some species which are distinctively limited to mammals, it has other species which reach maturity in aquatic birds only. Although individuals of some of the species of *Corynosoma*

from mammals may be found in aquatic birds there is a growing body of evidence (Lundström, 1942) to indicate that the physiological adjustment is not perfect since they cannot reach functional maturity in birds. Both the normal mammalian host and the unusual avian host secure the infective cystacanths through feeding on fishes which serve as a second intermediate host. *Bolbosoma*, the second genus of the *Polymorphinae* occurring in aquatic mammals, likewise utilizes fishes as the second intermediate host but no instance is on record of a representative of this genus appearing in a bird.

Habitats and Host Relations of Archiacanthocephala.—As parasites of land mammals, *Archiacanthocephala* confront more diverse conditions of the external environment than do the *Palaeacanthocephala* in the aquatic habitat. However, the well protected egg is the only stage in the life history ever exposed directly to the external environment since all of the other stages are given the shielding and screening effect of the body of a host. As is so often stated, the host provides the environment for the intestinal parasite so that local conditions of light, temperature, and moisture may in large measure influence the distribution of suitable hosts but could have little direct effect upon the parasite and its welfare or distribution. Since at least two distinctly different hosts, an arthropod and a mammal, are involved for all *Archiacanthocephala* here considered, there is extreme difference in the conditions under which the larval and the adult worm may live and to which each must be adapted.

For but few of the *Archiacanthocephala* of North American mammals is the outline of the life cycle complete and for many only the definitive host is known. Conditions under which the host mammals of these worms live inevitably involve the deposition of the eggs of the parasite in the feces of the host. Eggs thus eliminated are available to arthropods on or in the soil. Under the most direct life cycles the infected arthropods enter the digestive tract of a suitable mammal as food. This simple condition is characteristic of *Macracanthorhynchus* whose eggs in hog feces are available to white grubs and beetles in the soil. The entire succession of acanthor, acanthella, and cystacanth stages are passed in the body of the grub or beetle and are ready to infect the pig which feeds upon the infected insect.

On and in the soil the density of population of species of arthropods suitable as first larval host for *Archiacanthocephala* is rarely as great as the density of arthropod populations in the aquatic environment where *Palaeacanthocephalan* eggs are exposed to prospective hosts. Under these circumstances massive infections are often built up by the addition of second intermediate hosts in the life cycle. These must of necessity feed upon the larval host in order to pyramid the load of parasitic worms

carried to the definitive host intestine. In some instances the second intermediate host may not be an essential step in the life cycle. Thus in *Moniliformis*, which reaches maturity in rats and other rodents, the full developmental cycle may be satisfied in the body of a cockroach which is eaten by a rat to complete the cycle of the parasite. However, at times the infected cockroaches are eaten by amphibians or reptiles (Sandground, 1926) which may thus potentially represent a second intermediate host when the cystacanths of *Moniliformis* encyst in the tissues.

As an example of an essential second intermediate host the partially known life cycle of *Oncicola* will be mentioned. Unknown arthropods are postulated as the essential first intermediate host. An armadillo feeding on large numbers of the infected arthropods becomes second intermediate host to large numbers of cystacanths which become encysted in its viscera. At a single meal the dog or other carnivore which feeds upon the infected armadillo acquires a massive infection of *Oncicola* which become established in the intestine.

Differences in the physical conditions of the habitat may directly influence the distribution or abundance of potential hosts for *Archiacanthocephala* but these factors exercise little, if any, direct effect upon the distribution of the parasites themselves.

VII. ACCIDENTAL INFECTIONS AND UNUSUAL HOST RELATIONSHIPS

A generation ago parasitologists directed much attention to the extension of the lists of hosts for parasitic species and the converse expansion of lists of parasites, especially for animals of economic importance. Numerous papers were written with the sole purpose of recording a new host for a given parasite or a new parasite for a given host. At that time there was a very general belief that complete host lists and parasite lists were possible and desirable. It was then not generally recognized that in many instances the presence of a parasite may represent an accidental or incidental infection without biological significance in the life of either the host or the parasite. Especially in faunal surveys it is not always possible to distinguish between normal and incidental infections since the only available criterion is the ability of the host to bring the parasite to functional maturity. In an extensive field survey of the worm parasites of fishes of Oneida Lake, Van Cleave and Mueller (1934:318) summarized their evaluation of uncritically compiled host lists as follows: "We have placed little emphasis upon reporting new host records, since there are relatively few species of parasitic worms infesting fishes which may not occasionally find lodgment in any species of carnivorous fish of a given habitat." A similar statement could be made for the host-parasite relationships in all other groups of the vertebrates.

It is not at all uncommon to find in the intestine of mammals *Acanthocephala* which normally belong in some other host species or some other class of vertebrates. Many of these are what may be regarded as purely accidental introductions secured when the mammal ingested as food an infected intermediate host that is not normally included in its food habits. In such an instance the acanthocephalan may become attached to the intestinal mucosa either permanently or temporarily, depending upon the ability of the parasite to adapt itself to conditions found in an unusual environment.

At other times a vertebrate infected with either mature or immature intestinal *Acanthocephala* may serve a mammal as food. If the parasites escape the digestive action of the mammal, even mature worms may become established in the mammalian intestine. Although in such an instance the infection is purely accidental, as in the foregoing account, the

writer prefers to regard these as parasites "transplanted" to another host and to call them "transplants."

At times it is difficult or impossible to distinguish between some accidental infections and normal extension of host relationships. The occurrence of immature individuals of the avian genus *Centrorhynchus* in the digestive tract of cats constitutes an obvious case of accidental infection. However, the genus *Pseudoporrorchis* belongs to the same family (*Centrorhynchidae*) and most of its species have been reported exclusively from bird hosts, but fully mature individuals of *P. teliger* have been found only in mammals of Java (Van Cleave, 1949c). It still remains possible that an as yet undiscovered avian host may likewise serve this species.

As pointed out more fully in another section of this work, the host relations of species of the genus *Corynosoma* are most interesting. It is well established that some species of *Corynosoma* are restricted exclusively to mammals as definitive hosts and others to aquatic birds but in some instances the boundaries between the two host groups are transgressed, although apparently these instances are always recognizable as accidental infections.

In the literature there have been numerous instances recorded of the occurrence of unusual *Acanthocephala* in mammals and in the current investigation a considerable number of instances of accidental and transplanted infections have been encountered for North American mammals. These will be discussed in the following paragraphs.

GENUS *NEOECHINORHYNCHUS*

(*Eoacanthocephala*, *Neoacanthocephala*, *Neoechinorhynchidae*)

In its normal host relationships, all members of the genus *Neoechinorhynchus* occur as intestinal parasites of fishes, although one species (*N. emydis*) is restricted to North American turtles. A single instance of the occurrence of a representative of *Neoechinorhynchus* in mammals has come to the attention of the writer. Dr. Marvin C. Meyer submitted to the writer a number of specimens which he obtained from the autopsy of a raccoon (*Procyon lotor*) from an island off the coast of Maine. All of these were identified as *Neoechinorhynchus cylindratus* (Van Cleave), a normal parasite of fishes of that locality. There can be little doubt that the raccoon had fed upon infected fishes. After the bodies of the fish hosts had been digested the acanthocephalans were left free in the lumen of the digestive tract where they were able to establish themselves for at least a time. This is a clear instance of transplantation of *N. cylindratus* to the intestine of a mammalian host.

GENUS ECHINORHYNCHUS

(*Metacanthocephala*, *Palaeacanthocephala*, *Echinorhynchidae*)

The genus *Echinorhynchus*, as interpreted by modern taxonomists, is exclusively restricted to fishes as normal definitive hosts. The occurrence of representatives of this genus in the digestive tract of a mammal must invariably be regarded as an accidental infection, without any significance in the biology of the parasite. One instance of finding *Echinorhynchus gadi* Mueller in the stomach and intestine of a mammal has come to the attention of the writer in the present study. Mrs. Joanna Turner Krogsdale of State College, Pullman, Washington, submitted for identification specimens which she had found in the digestive tract of the raccoon (*Procyon lotor*). In submitting the material, she recorded the fact that the raccoons had been feeding on shore crabs, clams, and a fish (*Leptocottus armatus*). She further observed that only those which had been feeding on *Leptocottus* harbored *Acanthocephala*. Since this fish is a well known normal host for *Echinorhynchus gadi*, it is relatively certain that the parasites found in the raccoons were temporary transplants which remained in the digestive tract of the mammal after the fish host had been digested.

Mr. K. A. Neiland recovered a single cystacanth of what seems to be an unidentifiable species of *Echinorhynchus* from the tissues of the Oregon mole, *Scapanus townsendi*, at Oakville, Washington. Without doubt this is an accidental infection.

The occurrence of various species of *Echinorhynchus* in vertebrates that feed on fishes in nature is not uncommon. Captive animals fed on infected fish very often retain the worms in the digestive tract at least for a time. The tendency to harbor accidental transplants of *Echinorhynchus* and other species of fish acanthocephalans seems to be more often encountered in cold blooded vertebrates than in either birds or mammals.

GENUS CENTRORHYNCHUS

(*Metacanthocephala*, *Palaeacanthocephala*, *Polymorphidae*)

All available evidence indicates that representatives of the genus *Centrorhynchus* are always restricted to birds as normal definitive hosts. In the literature there are a number of instances recorded wherein specimens of *Centrorhynchus* are reported from mammals of various parts of the earth. Without exception these seem to be accidental infections obtained when the mammals ate an infected bird or an infected second intermediate host such as an insect, an amphibian, or a reptile. Evidences seem to indicate that limitation to birds as normal definitive hosts rests more upon food habits than upon any physiological condition within the intestine of a mammal inimical to the establishment of the worms. In a series of infection experiments, Read (1950) provided some of the evidence favoring this conclusion. He recovered mature individuals

of *Centrorhynchus spinosus*, a normal parasite of birds, from rats experimentally fed on cystacanths taken from a garter snake which serves as a second intermediate host or paratenic host (Baer, 1951:12). From the results of this experiment Read concluded that there is a low degree of host specificity in the genus *Centrorhynchus*.

In the writer's collections there are included several series of *Centrorhynchus* cystacanths taken from amphibians and reptiles of North America but there have been only a few instances in which the parasites have been recovered from mammals. Mr. C. M. Senger has submitted specimens of an undetermined species of *Centrorhynchus* which he found in the intestine of a raccoon (*Procyon*) and of a shrew (*Neosorex*) at Portland, Oregon. Cystacanths of apparently the same species were found in several species of amphibians (*Rana*, *Ensatina*, *Triturus*) in the same area. The avian acanthocephalan fauna of the Pacific northwest is so poorly known that there seems to be no possibility at this time to identify the cystacanths of *Centrorhynchus* from amphibians and mammals.

GENUS POLYMORPHUS

(*Metacanthocephala*, *Palaeacanthocephala*, *Polymorphidae*)

Polymorphus is the type genus of the subfamily *Polymorphinae* which includes the genus *Corynosoma*, so commonly found in aquatic birds and mammals. In so far as is known, representatives of the species of *Polymorphus* are rather rigidly restricted to birds as normal definitive hosts. In the literature there is at least one reference (Knight, 1951) to the occurrence of *Polymorphus* in the intestine of a mammal, and other instances will be recorded here for the first time. There is no doubt that these must be regarded as accidental infections. Immature worms may be acquired when the mammal swallows an infected first or second intermediate host but it seems doubtful that these could ever reach sexual maturity. It is more difficult to explain the presence of fully mature females of *Polymorphus* in a mammal unless the mammal might have fed upon an infected bird whose mature parasites became transplanted to the intestine of the mammal. This assumption is supported by two references in the literature. Hollister (1911) records that muskrats sometimes eat dead birds. More recently Smith (1938) exposed five young starlings and three adult English sparrows to muskrats confined in pens and found that within three hours all of the starlings and two of the sparrows had disappeared. These two sets of observations offer ample proof that mature acanthocephalan parasites of infected birds can be transplanted to muskrats. In the literature and in field studies the incidence of occurrence of mature individuals of *Polymorphus* in mammals is so low that normal passage of immature worms in intermediate hosts taken as

food seems to be ruled out as a possible explanation for the presence of gravid female parasites in mammals.

The writer has examined slides of Acanthocephala prepared by Mrs. Iola Musfeldt Knight in her study (1951) of the parasites of muskrats in British Columbia. This material included a total of seven worms from the intestines of four individuals and all of these were from the same general area. No Acanthocephala were found in 138 muskrats originating from four other collecting areas. All seven of the worms represent a single undetermined species of the genus *Polymorphus*. Some of the individuals in this series are gravid females whose bodies are filled with mature eggs. As suggested above, it is at least a possibility that these might have been ingested as mature worms that became at least temporarily attached, as transplants, to the intestinal wall of the muskrat.

More recently, Dr. Robert Rausch and Mr. Bert Babero have collected a few immature specimens of an undetermined species of *Polymorphus* from the intestine of the muskrat of Alaska. In both of these instances the parasites are so small and so immature that they might have reached the digestive tract of the mammal accidentally when infected arthropods or other intermediate hosts were fortuitously included along with vegetation ingested as food.

Specific identification of immature specimens of the genus *Polymorphus* is impossible because in several species the form and size of the proboscis change radically after the young adult becomes established in the intestine of the definitive host (Van Cleave, 1952b). Specific identification of the immature specimens of *Polymorphus* from muskrats of Alaska must await the final study and identification of extensive collections of members of this genus from Alaskan birds furnished to the writer by Messrs. Rausch, Schiller, Williams, and Babero.

GENUS *CORYNOSOMA*

(*Metacanthocephala*, *Palaeacanthocephala*, *Polymorphidae*)

Since the genus *Corynosoma* has many species that are normal parasites of mammals, it may seem inconsistent to include this genus in the records of accidental infections. However, as emphasized in another section of this same work, there are numerous records of mammalian species of *Corynosoma* occurring accidentally in birds where they are unable to reach full maturity. The reverse of this relationship is not so frequently encountered but the collections available to the writer include one instance of the accidental occurrence of *C. constrictum*, an avian species, in the digestive tract of two mink (*Mustela vison*, var.?). This record is from the field investigations of Dr. Robert Rausch in the Horicon Marsh, Wisconsin.

The infrequency of the occurrence of this species in mammals of its

normal habitat indicates that the intermediate host of *C. constrictum* is probably not commonly included among the organisms that serve the mink and other mammals as food.

GENUS PROSTHENORCHIS

(*Metacanthocephala*, *Archiacanthocephala*, *Oligacanthorhynchidae*)

The genus *Prosthenorchis* is occasionally introduced into North America when anthropoids are imported for zoological gardens and for use in experimental laboratories. There is no evidence to indicate that the members of this genus have become permanently established in nature as a component of the North American fauna. However, the writer has examined numerous collections of *Acanthocephala* taken from New World monkeys in zoos and in laboratories and all of those examined belong to the species *Prosthenorchis elegans* (Diesing). The monkeys have clearly carried the infection from their original habitat in South or Central America where *P. elegans* is endemic.

In only one instance is there evidence that potential foci for reinfection have become established within a zoo, but the problem has not been examined critically for many localities where the worms have been introduced. Dr. J. Teague Self collected specimens of *Prosthenorchis* from a spider monkey (*Ateles* sp.) at the Tulsa, Oklahoma, zoo and submitted them to the writer for identification. All were recognized as *P. elegans*. At the same time he sent a number of preserved cockroaches from the same building, many of which were infected with cystacanths of *Prosthenorchis*. From one cockroach 14 cystacanths of *P. elegans* were removed. It is thus obvious that under conditions where suitable intermediate hosts are found *P. elegans* may become established but there is no evidence that the infection has spread to regions outside the building where introduced or to native North American mammals.

The situation here recorded is similar to that described by Brumpt and Urbain (1938) when they found *P. elegans* and *P. spirula* established in the Paris Zoological Garden with larvae of both species occurring in a cockroach (*Blatella germanica*). However, the American incident differs from the French in that *P. spirula* has never been recognized in the worms taken from hosts in North America.

In the literature there has been considerable confusion regarding the species which has gone under the name *P. elegans*. Both Meyer (1931a) and Dollfus (1938) have pointed out the fact that the concept of *P. elegans* included in the early works of Travassos (1915, 1917) does not conform to that given by Diesing, the original describer. However, these two authorities have offered divergent solutions to the problem. Dollfus regarded Travassos' concept of *P. elegans* as the direct equivalent of *P. spirula* (Olfers) but Meyer interpreted it as a distinct, previously un-

recognized, species to which he applied the name *P. sigmoides*. The most recent reviser of the genus *Prosthenorchis*, Machado Filho (1950) accepted the nomenclature of Meyer. Although the present writer received specimens of "*P. elegans*" from Travassos, the available descriptions of *P. sigmoides* and *P. spirula* are so unsatisfactory that the Travassos material might fit either description. The writer is therefore inclined to believe that *P. sigmoides* is a synonym of *P. spirula*.

Parasites Misplaced in the Host.—It is very commonly stated that all *Acanthocephala* normally reach maturity only in the lumen of the digestive tract of a vertebrate host. However, mature individuals of both sexes are occasionally found in the body cavity of a vertebrate host. When a single gravid female worm is found in this situation it is not possible to explain her viable eggs in the absence of a male on the basis of natural early elimination of males as is the obvious explanation for gravid females appearing without males in the digestive tube of the host. All evidence points to the necessity of assuming that the female had been impregnated by a male while both were still residing within the intestine of the host. Later, active movements of the female and operation of the proboscis perforated the intestinal wall and allowed the fertilized female to enter the body cavity. There is strong evidence to indicate that very young immature worms that penetrate the intestinal wall of the host cannot become fully mature in the body cavity.

De Guisti (1949) has demonstrated experimentally that when a young acanthella of *Leptorhynchoides thecatus* within the body of an arthropod host is introduced into the digestive tract of a suitable vertebrate host (a fish) it is unable to become established there but penetrates the wall of the intestine and becomes encysted in the viscera without any appreciable advance toward maturity. Thus the same host individual of *L. thecatus* may be a normal definitive host carrying mature worms in the intestine and at the same time serve as a second intermediate host with encysted larvae in the viscera. While this condition has not been demonstrated experimentally for mammalian *Acanthocephala*, the pattern of development throughout the phylum is so uniform that it is fairly safe to assume that immature larvae taken into the digestive tract of a mammal perforate the intestinal wall and encyst in the viscera. Price (1929) reported the occurrence of young individuals of *Oncicola canis* encysted in the esophagus of turkey poults. The turkey is not a normal definitive or intermediate host of *Oncicola* but when a turkey fed upon arthropods infected with acanthellas of *Oncicola* the immature worms were not able to attach themselves but penetrated the wall of the digestive tract to become encysted without reaching maturity in that host.

Several investigators have reported adult acanthocephalans in the body cavity of mammals. Thus Rausch (1946) found adults of *Macracantho-*

rhynchus hirudinaceus in the body cavity as well as in the lumen of the intestine of the fox squirrel. Harwood and Cooke (1949) found immature specimens of the same parasite in the body cavity of a fox squirrel. Peery (1941) reported the recovery of several mature males of *Moniliformis* from cysts in the abdominal viscera of fox squirrels of Oklahoma. In these instances, which are but samples of records in the literature, there seems to be little doubt but that the metamorphosed worms had ruptured the intestinal wall to gain access to the body cavity.

Normal Extension of Host Relations.—In addition to the accidental infections, mentioned above, there are often encountered instances in which apparently new normal host relationships become established. These are especially pronounced in cases involving introduction of a parasite into the fauna of a new territory either by natural extension of the range of its normal hosts or by the agency of human introduction of infected normal definitive hosts. For establishment in a new territory, there is a demand for a fine balance between the ability of the parasite to become adapted to physiological conditions existing in a new potential host and the ecological conditions which are conducive to bringing the parasite and host together. A readily observable instance is the adaptation of the thorny-headed worm of the hog (*Macracanthorhynchus hirudinaceus*) to conditions found in squirrels (Rausch, 1946; *et al.*) and other native mammals. The newly acquired definitive hosts infect additional intermediate hosts and thereby enhance the probability of survival of the species of parasite in the locality.

Vectors.—Vectors or mechanical carriers play no immediate role in the life history of acanthocephalans, yet they probably have greater importance than has heretofore been recognized. Glasgow and De Porte (1940) demonstrated that viable eggs of *Macracanthorhynchus hirudinaceus* were recovered from the droppings of pigeons. Thus though birds may have no direct part in the development of members of this species they may be important passive transport agents effective in widening foci of infection. Mechanical carriers of this type could readily explain the rapid spread of introduced species of Acanthocephala.

VIII. RELATIONS WITH FAUNAS OF ADJACENT CONTINENTS

Availability of Records.—Except for *Macracanthorhynchus* which occurs in domestic swine and for *Moniliformis* of rats, the literature on North American *Acanthocephala* of mammals is very limited and in most instances it is restricted to records of the occurrence of individual species or to surveys concerning one or a few genera. This is in sharp contrast with the voluminous literature on these parasites and their diversification in South America. Although the number of species in mammals of northern Europe and Asia is small, there has been frequent mention of these forms in the literature.

Continental Distribution in Marine Mammals.—The *Acanthocephala* of marine mammals of North America show very few evidences of relationship with the South American fauna. In part, this might possibly be attributable to the fact that there have been but few studies on these hosts in South America and the few that have been made concern the forms bordering on the Antarctic realm. In a superficial comparison of the Arctic and Antarctic *acanthocephalan* faunas, based largely on the literature, Meyer (1931b) recorded no species common to the two polar realms. It seems probable that the much longer list of species from the Arctic realm is due to the fact that scientific programs have been more extensively developed in Northern European countries than in the parts of the southern hemisphere contiguous to the Antarctic and that scientific exploration of the north polar region has been very actively pursued for several generations.

Continental Distribution in Land Mammals.—A small number of the species of *Acanthocephala* found in land mammals are essentially cosmopolitan in distribution. One species in each of the genera *Moniliformis* and *Macracanthorhynchus* has attained this dispersal. Most of the species occurring in land mammals of North America are closely related to those of South America and through the fauna of that continent show relationships with the *Acanthocephala* of Africa and southern Asia. On the contrary, the *Acanthocephala* of marine mammals of North America show immediate relationships with the northern Eurasian faunas and have practically no direct connection with the faunas of South America, Africa, and southern Asia. This generalization is supported by the fact that the species found in land mammals of North America are most of them limited to the southwestern states where they occur in mammals

either phylogenetically or ecologically near to those of the fauna of Central and South America. In addition to the widely distributed genera *Macracanthorhynchus* and *Moniliformis* mentioned above, the genera *Oncicola*, *Pachysentis*, *Hamanniella*, and *Echinopardalis* of the *Archiacanthocephala* are found in both North and South America. Few of the recent land mammals distinctive of southwestern United States have extended their distribution to other parts of North America. It seems evident then that neither suitable arthropod nor vertebrate hosts of wide geographical dispersal are in contact with the areas which the parasites have occupied and so the distinctive acanthocephalan parasites of land mammals have been unable to extend their geographical distribution into new territory by way of newly acquired host relationships.

Distinctive Genera.—Two genera commonly regarded as distinctive of land mammals of South America (*Prosthenorchis* and *Echinopardalis*) have never been reported previously as established in North American mammals. The former of these occurs primarily in new world monkeys and occasionally in other mammals as definitive hosts. On the basis of high variability, possibly associated with host differences, Machado Filho (1950) has recognized at least a score of species in the genus *Prosthenorchis* with the possibility that some of these occur in Africa. *Echinopardalis* is reported from a North American mammal for the first time in the present report.

Gigantorhynchus, with its single species *G. echinodiscus* (Diesing), is particularly distinctive of South America where it is confined to endemic anteaters as definitive hosts. At the extreme margin of its geographical distribution, *Gigantorhynchus* seems unable to become adapted to other mammals. Dunn (1934) found it only in anteaters in Panama, and Cameron (1939) found it restricted to anteaters of the island of Trinidad off the north coast of South America.

In contrast with the records of genera and species of *Archiacanthocephala* largely restricted to South America, there is not a single genus of *Archiacanthocephala* peculiar to the land mammals of North America. Most of the evidence seems to support the belief that the *Archiacanthocephala* became diversified in the land mammals of Africa and South America in an earlier geological period when the two continents were connected and that there has been but slow extension of any of these forms into the North American continent.

On the continents of Europe and Asia, the *Acanthocephala* of mammals are represented by a relatively small number of species, even when the imperfectly known species are included. Thus in Europe, except for *Macracanthorhynchus* and *Moniliformis*, only one distinctive species from land mammals is widely recognized, *Nephridiorhynchus major* from hedge-hogs. Some faunal lists include nine or more additional species

but all of these are names proposed by early investigators and never again recognized. Most of these are so imperfectly known that it is impossible to assign them to any genus in the modern system of nomenclature.

For the poor representation of Archiacanthocephala in the land mammals of northern Europe it has always seemed possible that lack of comprehensive surveys might be responsible for the infrequency of records. For many generations the attention of investigators of northern Europe has been directed primarily to the parasites of fishes with only incidental mention of Acanthocephala from other hosts. In a recent comprehensive report on the acanthocephalan fauna of Sweden, Lundström (1942) gave the results of the examination of 195 individual mammals representing 28 species. He recorded the discovery of worms in each of two species of mammals but in his investigation he did not include marine mammals. Both of the recorded infections were accidental. One specimen of *Sorex aureus* carried in the body cavity a single immature individual of *Prosthorhynchus genitopapillatus*, a normal parasite of the intestine of birds. A single individual of *Lutra lutra* contained 29 specimens of *Acanthocephalus lucii* in the stomach and intestine and one of *Ac. anguillae* in the stomach. Both of these are normal parasites of the intestine of fishes and without doubt the adult worms had become temporarily established in the mammalian host when the normal fish host was taken as food. Although Lundström did not include marine mammals in his survey, he encountered immature individuals of both *Corynosoma semerme* and *C. strumosum* in the fishes of Sweden and an accidental infection by *C. strumosum* in a bird (*Sterna hirundo*). Similarly, although *Bolbosoma* had been reported previously from whales of Sweden, Lundström did not find any additional evidence of the occurrence of this genus in other mammals.

It is thus clear that the lack of records of Acanthocephala in land mammals of northern Europe is not due to inadequacy of sampling.

Marsupials as Hosts.—Although the primitive mammals of North and South America, especially the marsupials, as well as many of the insectivores and edentates of the Americas, Africa, Asia, and Europe are commonly hosts for Archiacanthocephala, there is no record of the regular occurrence of a member of this order in any of the highly diversified marsupial fauna of Australia.

Absence of Archiacanthocephala from the distinctive marsupial fauna of Australia might be due to the operation of any one of several conditions. (1) The Archiacanthocephala may have established their relations with mammals serving as definitive hosts at a time after the Australian continent became isolated, or (2) the marsupials which migrated from the Holarctic region into Australia were unable to establish

satisfactory relations with suitable arthropod hosts in the course of their migration. According to the second of these possibilities, the primitive Holarctic precursors of all present-day marsupials might have been hosts to Acanthocephala. As one branch of this stock occupied North and South America to give rise to the Didelphoid marsupials these continued to inhabit territory where suitable arthropods and other hosts were available to maintain infections. On the other hand, the stem which ultimately gave rise to the five distinct families of Australian marsupials may have entered territory where suitable arthropods were not available as first intermediate hosts or if present they were not included in the food of the marsupials. (3) Still another possibility is that the precursors of present-day marsupials might have been devoid of distinctive acanthocephalan parasites. In the Americas they could have gained infection secondarily through association with other susceptible mammals, while in Australia there were no higher mammals through which infection could be passed to the marsupials.

Avenues for Dispersal.—The land bridge connecting North and South America has served as an avenue for the passage of terrestrial mammals from one continent to the other. Acanthocephalan parasites are transported by the migrating mammals and if suitable intermediate hosts are present in the new environment the extension of the geographical range of the mammal establishes a corresponding extension of the range of the parasite with the possibility that additional potential hosts may be encountered in the new locality.

There is no direct evidence to suggest the possibility that marine mammals from the southern hemisphere have been immediately responsible for the introduction of any acanthocephalan parasites into the North American fauna. Nor is there any evidence that Acanthocephala of marine mammals of the northern hemisphere have extended their range into South America.

The Arctic seas, connecting directly with both the Pacific and the Atlantic waters, form a highway for distribution of marine mammals of North America and Eurasia. Lack of physical or other barriers to the movement of those marine mammals which carry Acanthocephala, permits at least some species of the parasites to occur normally in the seas of all continents in the Holarctic realm, wherever suitable intermediate hosts are available.

Distinctive species of Acanthocephala are essentially lacking in the land mammals of the northern regions of Eurasia and North America. The few forms which have become adapted to life in land mammals are primarily the parasites of aquatic animals which have become secondarily adapted to the land dwellers. Examples are found in the species of *Corynosoma*, normally appearing in seals and other aquatic mammals,

which on occasion has been found in sledge dogs of the arctic and in minks. Fishes, the second intermediate hosts of *Corynosoma*, transmit the infection by normal food chains to seals but when in nature or by human agency other mammals feed upon infected fishes the worms are able to establish themselves in an unnatural host. Although the Acanthocephala of marine mammals seem to have become widely dispersed by natural agencies through the northern part of the Holarctic realm, there is no species exclusively distinctive of land mammals which has travelled by way of the land route between northern Eurasia and North America.

Limits to Distribution.—The geographical distribution of Acanthocephala is not commonly determined directly by physical or physiographical barriers as it is for many free living organisms. In establishing limits to geographical distribution of these forms, the external environment plays no direct role except as it in turn circumscribes the distribution of suitable hosts. For these parasites, the problem becomes still further complicated because continuous distribution of a normal definitive host does not necessarily indicate identical geographical distribution for its parasite throughout the same territory. In species of Acanthocephala with the least complicated life histories, a minimum of two different species of essential hosts is always involved and these must occur within the same territory because the transfer from the arthropod intermediate host to the vertebrate definitive host is invariably through the former serving as food for the vertebrate. Under these simplest conditions, infection through any other agency is wholly unknown. The two hosts are thus equally responsible for setting the limits to the dispersal of the parasite. When the two essential hosts have distribution that is not identical, the focus of distribution of the acanthocephalan coincides with the area where the respective distributions of the two hosts come into contact or overlap. However, in many instances the host relations are not absolutely specific so that in various parts of its range an acanthocephalan may have different species of arthropod intermediate hosts or of vertebrate definitive hosts. Thereby the geographical range of the parasite may exceed the distribution of any one of its hosts. In addition to the normal extension of the geographical range of the parasite, accidental or fortuitous hosts may be acquired but these are often blind alleys in the life history, since commonly these accidental hosts are unable to permit the worms to complete the cycle of normal development. This may be due to lack of physiological adaptation between parasite and host or equally it may be attributable to the fact that normal food chains do not bring the larval worms within the intermediate hosts into the food habits of a suitable definitive host.

Faunas to the South.—Unfortunately, very little is known about the acanthocephalan fauna of Mexico and Central America, consequently it

is difficult, and at present impossible, to determine if distribution of any given species is continuous between North and South America. Many of the species known to occur in land mammals of South America have been described so briefly and inconsistently that direct comparison of North American specimens with descriptions of South American representatives is extremely hazardous. In spite of the inadequacy of the literature there are apparently authentic records of a few species which occur in land mammals of both North and South America. On the other hand, although there is no record of any species living in marine mammals common to North and South America these forms have been very inadequately studied.

The Holarctic and Arctic Realms.—In contrast, the relationships of the fauna with other continents of the northern hemisphere show the opposite relationship. Except for the practically cosmopolitan species there is no record of continuous distribution of characteristic parasites of land mammals in the Holarctic but there are numerous interrelations of the parasites of marine mammals through the Holarctic realm.

The acanthocephalan parasites of marine mammals are most abundant in the Arctic realm of North America and along the Pacific coast where physical and physiographical barriers to distribution of the hosts are less pronounced than for land mammals. Correlated with this fact, many of the genera and some of the host species found in America are identical with those of the Eurasian polar region and carry the same species of acanthocephalan parasites. On the American continent, some of these parasites have acquired additional hosts peculiar to the American fauna and at the same time other species of the parasites have become diversified and are found only in species of hosts which are of limited geographical distribution on this continent.

Comparisons of Palaeacanthocephalan Faunas.—The mammalian hosts of Palaeacanthocephala are either aquatic or have direct association with the aquatic environment. This statement is correlated with the fact that the eggs of the parasite are usually liberated in the water where they are eaten by aquatic arthropods capable of serving as the first intermediate host. Thereby the life cycle is essentially confined to definitive hosts which feed upon aquatic arthropods or upon second intermediate hosts which in turn utilize aquatic arthropods as food. Consequently, the members of this order which are parasitic in mammals are not as sharply restricted to continental limits as are the Archiacanthocephala which live in land mammals.

Both of the distinctive genera *Corynosoma* and *Bolbosoma* are almost world-wide in the composite distribution of their species. Some species have attained very wide geographical distribution although others occupy distinctly localized territory. Especially does the genus *Corynosoma* seem

to have undergone speciation which clearly differentiates the Holarctic fauna from that of regions contiguous to the Antarctic. As has been mentioned elsewhere in this work, differences in the physiographical environment seem to be less important than the factors of geographical isolation and host isolation in the directing of speciation of Acanthocephala.

Comparisons of Archiacanthocephalan Faunas.—In the literature and in the present article there are records of seven genera of Archiacanthocephala of land mammals occurring commonly in South America but reported likewise from North America: *Macracanthorhynchus*, *Moniliformis*, *Echinopardalis*, *Pachysentis*, *Oncicola*, *Hamanniella*, and *Travassosia*. As has been shown earlier, *Travassosia* is a direct synonym of *Hamanniella*. Thus the number of valid genera common to the two Americas is reduced to six. Two of these genera have attained practically world-wide distribution (*Macracanthorhynchus* and *Moniliformis*). Each is represented on the two continents by identical species, although for each an additional distinctive species is known for North America only (*Macracanthorhynchus ingens* and *Moniliformis clarki*). Although the synonymy is extremely confused, it seems probable that two species of *Moniliformis* are indigenous to South America but no species of *Macracanthorhynchus* is limited to that continent. Other species of *Moniliformis* occur in Europe, in Africa, and in Asia, yet the status of some of these is doubtful. Thus the genera *Macracanthorhynchus* and *Moniliformis* have been dispersed to all major regions of the earth and evolution has proceeded independently in several areas to establish new species.

A single North American record of *Pachysentis* has been identified in the literature as identical with a South American species, *P. canicola*. Of the three known species of this genus, two are indigenous to Africa while the third, *P. canicola*, probably arose in South America and has extended its range into North America. It therefore seems probable that *Pachysentis* originally underwent speciation in South America and Africa and has only recently invaded the southern border of North America. In similar manner *Echinopardalis* has recently entered North America.

Oncicola is represented in North America by a single species, *O. canis*, parasitic chiefly in dogs and coyotes. This same species has been reported from members of the cat family in South America where different species of the genus are commonly found in native cats. Meyer (1932) has recorded three species, *O. onicola*, *O. campanulata*, and *O. macrurae* from South America. Witenberg (1938) reviewed the literature and, after study of specimens of several of the species, recognized nine nominal species, some of which are of doubtful status. One species is from Africa, one from Palestine, two are from islands of the south Pacific off the Malay Peninsula and one is based upon museum specimens for which

the place of origin is unknown. It is thus evident that *Oncicola* has wide geographical distribution and that the only species found in North America has been identified in the South American fauna where several other species are endemic.

The concept of the genus *Hamanniella* was first recognized by Travassos (1915b), but due to homonymy and several misspellings the exact form of the name was uncertain for some time. In it were included one species from didelphoid marsupials and one from armadillos of South America. Later, Van Cleave (1925) placed *Echinorhynchus tortuosus* of Leidy, from the North American opossum, in the genus *Hamanniella*.

Incidentally, Chandler (1946) has reported young adults of a species which he tentatively identified as *H. tortuosa* from the intestine of *Dasypus*. All evidence seems to indicate that *Hamanniella* has never extended its geographical distribution beyond the confines of South and North America. As here emended by inclusion of the genus *Travassosia* within its confines, the genus *Hamanniella* includes at present four species parasitic in didelphoid marsupials and dasypodid edentates of the Americas. Although these two host groups are not closely related phylogenetically, they are similar in their ecology, and under proper conditions infections might pass from one group to the other.

IX. PREVIEW OF THE CLASSIFICATION AND KEYS

The Class Metacanthocephala.—By way of summary, the Acanthocephala known to reach sexual maturity in mammals of North America belong to two distinct orders, the Archiacanthocephala and the Palaeacanthocephala both of which are within the class Metacanthocephala. As emended by Van Cleave (1936), the Archiacanthocephala are essentially the equivalent of the Gigantorhynchidae as conceived by Hamann and developed by subsequent investigators. As outlined by Meyer (1932:26) the Archiacanthocephala includes five families, four of which have species occurring in mammals. In the present reconsideration the writer has been unable to justify the family Pachysentidae inasmuch as its members show no features other than relative morphological characters for separating it from the family Oligacanthorhynchidae. Consequently the Pachysentidae as a family are eliminated from consideration. Thus only four families remain in the Archiacanthocephala (Gigantorhynchidae, Oligacanthorhynchidae, Moniliformidae, and Apororhynchidae). Of these only the first three have representatives found in mammals and the Gigantorhynchidae are not found in mammals of North America. Consequently the Oligacanthorhynchidae and the Moniliformidae are the only Archiacanthocephala considered in the taxonomic section of this article.

The current arrangement of the Palaeacanthocephala of mammals of North America presents no problems of synonymy in the higher categories similar to that evident in the taxonomy of the Archiacanthocephala. The two genera *Corynosoma* and *Bolbosoma* are clearly defined, sharply delimited from other genera of the order and both genera fall naturally in the subfamily Polymorphinae.

As a preview of the classification of the Acanthocephala under consideration in the present study, the following keys are presented as a guide to the recognition of the genera and higher categories. It must be borne in mind that for the keys to families and genera only those groups encountered as adults in mammals of North America are included.

Key to the Classes and Orders of the Phylum Acanthocephala.—In this key the proposal of Byrd and Denton (1949:408) for the recognition of a separate order for the genus *Apororhynchus* is considered as unnecessary, since the genus fits consistently within the Archiacanthocephala.

1. (a) Body wall and lemnisci provided with a very small number of giant subcuticular nuclei. Cement gland of male a single syncytial organ with a specialized cement reservoir. Proboscis receptacle a closed sac whose wall consists of a single muscular layer. Main trunks of the lacunar system dorsal and ventral. Never with specialized excretory organs. Normal definitive hosts always cold blooded vertebrates.—Class EOACANTHOCEPHALA—2.
- (b) Body wall and lemnisci provided with numerous amitotically fragmented nuclei or with a few grouped amoeboidal giant nuclei. Cement glands of male consisting of several separate glands without a cement reservoir. Proboscis receptacle with a conspicuous ventral cleft and only one conspicuous muscular layer or a closed sac with two concentric muscular layers. Main trunks of the lacunar system either lateral, or dorsal and ventral, or dorsal only. Often with specialized excretory organs associated with genital tract. Normal definitive hosts include all groups of vertebrates.—Class METACANTHOCEPHALA—3.
2. (a) Trunk provided with cuticular spines of varied arrangement.—Order GYRACANTHOCEPHALA.
- (b) Trunk invariably lacking cuticular spines.—Order NEOACANTHOCEPHALA.
3. (a) Males with 8 separate cement glands. Adults in birds and mammals. Main trunks of lacunar system dorsal and ventral or dorsal. Often with special excretory organs. Ligament sacs of female dorsal and ventral, persistent.—Order ARCHIACANTHOCEPHALA.
- (b) Males with less than 8 but more than 1 cement glands. Adults in all groups of vertebrates. Main trunks of lacunar system usually lateral. Never with special excretory organs. Ligament sacs of female usually ruptured so that eggs develop in body cavity.—Order PALAEACANTHOCEPHALA.

Key to the Families and Genera of Archiacanthocephala Occurring as Normal Adult Parasites in Mammals of North America.—

1. (a) Proboscis short, globular.—Family OLIGACANTHORHYNCHIDAE.—3.
- (b) Proboscis cylindrical.—2.
2. (a) Proboscis receptacle a closed muscular sac with its external musculature arranged in conspicuously diagonal, spiral bands. Proboscis hooks sickle-shaped without conspicuous differentiation between those of the anterior and posterior regions. Roots of proboscis hooks not sharply set off from thorns. Trunk usually showing pseudosegmentation.—Family MONILIFORMIDAE. Sole genus, MONILIFORMIS.
- (b) Proboscis receptacle bearing a conspicuous ventral cleft through which the proboscis invertors emerge as the retractors of the re-

ceptacle. Proboscis hooks clearly differentiated into an anterior series of heavy recurved hooks with prominent reflected roots and nearly straight thorn-like hooks without reflected roots covering the cylindrical or truncated conical base of the proboscis.—Family GIGANTORHYNCHIDAE. Genus GIGANTORHYNCHUS, the only genus occurring in mammals, not found in North America.

3. (a) Proboscis hooks in 12 spiral rows of 8 or 9 hooks each. Body of preserved specimens cylindrical, short, thick with greatest trunk diameter near anterior end. Diameter reducing rapidly anteriorly to that of the neck but only slightly toward posterior extremity. Testes contiguous and in contact with the cement glands.—Genus PACHYSENTIS.
- (b) Proboscis hooks in six spiral rows.—4.
4. (a) Body relatively short, plump, greatest diameter near anterior one-fourth. Male organs extend into front half of body cavity, testes contiguous or overlapping and in contact with or overlapping the cement glands.—Genus ONCICOLA.
- (b) Body relatively long, many times the maximum diameter. Testes not in contact and considerable distance anterior to the cement glands.—5.
5. (a) Trunk attenuated posteriorly for considerable distance; anteriorly quickly reduced in size to meet that of the narrow neck.—Genus MACRACANTHORHYNCHUS.
- (b) In preserved individuals, the posterior extremity of the cylindrical trunk much greater diameter than anterior extremity. Anterior extremity very greatly attenuated for a long distance to meet the diameter of the small neck.—GENUS HAMANNIELLA.

Key to the Genera of Palaeacanthocephala Known to Occur in Mammals of North America.—All mammalian Acanthocephala of North America belonging to the order Palaeacanthocephala are included within the single subfamily Polymorphinae. The members of this subfamily are the only ones of this order with cuticular spines on the trunk which reach maturity in the intestine of birds and mammals.

1. (a) Main part of trunk usually long, cylindrical in preserved condition. An enlarged, bulbous, spine-covered anterior extremity of the trunk is connected with the remainder of the trunk by a very narrowly attenuated region of fairly uniform diameter. Attenuated portion of trunk posterior to spine field not clearly developed in juvenile worms. Trunk spines confined to the inflated bulb of the trunk, usually in two separate fields, never extending along the ventral surface of the trunk and never surrounding the genital orifice of either sex.—Genus BOLBOSOMA.
- (b) Trunk usually with an inflated, spine-clad anterior extremity of

larger diameter than remainder of trunk from which it is never set off by an attenuated region. Spines on anterior part of trunk usually in two fields or collars of which the posterior may extend farther along the ventral surface than on the dorsal, often continuing to the genital extremity. In many species the genital spines around the genital orifice are discontinuous with the anterior spination and often may be withdrawn from the body surface by the introversion of a genital vestibule.—Genus CORYNOSOMA.

X. NORTH AMERICAN COLLECTIONS OF PALAEACANTHOCEPHALA OF MAMMALS

Early American Records.—Excluding the species living as adults in birds, there have been but few records of the occurrence of representatives of the genera *Corynosoma* and *Bolbosoma* in North America. In fact, none of the early investigators mentioned adults from mammals that can now be recognized as attributable to either of these genera. Although he listed them as species of *Echinorhynchus*, Linton (1891) described immature specimens from marine fishes. In spite of the inadequacy of the descriptions two of these are now recognizable as members of the genus *Corynosoma* living in their second intermediate hosts. One of these Linton identified as *Echinorhynchus incrassatus* Molin, but his identification was obviously in error. In his description Linton mentioned the fact that his specimens carried body spines and although this feature was contrary to the condition in *E. incrassatus*, Linton minimized that difference on the ground that he regarded body spines of immature worms as not of much importance in taxonomy. He explained this position as based upon his observation that body spines are frequently lost in the adult stage. However, he offered no direct evidence supporting this conclusion and no other investigator has supplied the evidence.

One other species which Linton (1891) mentioned as having body spines was *Echinorhynchus carchariae* Linton, 1891. From his drawings this is recognizable as probably belonging to the genus *Corynosoma*. It was based upon a single immature specimen from a marine fish. This species has never been recognized by any subsequent writer. Meyer (1932:253) listed it with the species "Delenda." The original description is so incomplete that there is no value to be derived from attempting to recognize *E. carchariae* as either a distinct species or as a direct synonym.

It is evident that Linton prepared the plates for his 1891 report before final editing of the text. In the explanation of his figures he assigned the nude name *Echinorhynchus odontaspidis* to a specimen which he figured as drawings 81 and 82 but in the text he attributed these figures to *E. carchariae*.

Echinorhynchus serrani Linton, 1891, an immature worm from a marine fish, has body spines but the body shape is incompatible with that of the genus *Corynosoma*. No additional record of the occurrence of this species appears in the literature except as direct reference to the original

description. Apparently on that inadequate description alone, Porta (1905:181) regarded *E. serrani* as an immature stage of *Bolbosoma aurantiacum*. Meyer (1932:87) accepted the specific synonymy although he regarded *B. vasculosum* (Rudolphi, 1819) as the valid name for the species.

Stiles and Hassall (1894) prepared a preliminary catalog of all the collections of parasites available to them in the United States. In that list they mentioned but one specific determination of an acanthocephalan from a marine mammal of this continent. This was given as *Echino-rhynchus pellucidus* from a whale and as mentioned above this is now known under the name of *Bolbosoma vasculosum* (= *B. aurantiacum*). Leidy (1890) had mentioned the same collection of worms from *Mesoplodon bidens* (= *M. sowerbiensis*) taken by Dr. Cooper Curtice of Washington, D. C.

In his listing of the Acanthocephala by continents, Meyer (1933) covered the world literature very consistently. In his list for North America (1933:394) he cited *Corynosoma strumosum* from the Pacific as the only acanthocephalan from a marine mammal of this continent. That record is based upon a paper by Ball (1930) recording *C. strumosum* from *Phoca vitulina richardii* (= *P. vitulina*), the California harbor seal, taken in Ventura County, California.

In the later literature, knowledge of the Palaeacanthocephala from marine mammals of North America developed very slowly. The readiness to assume that the acanthocephalan fauna of these hosts in America would be identical with those found in the wide ranging species of the better-known European Arctic and sub-Arctic fauna seems to have served as a deterrent to any normal curiosity regarding this fauna in the new world. When this assumption is coupled with the realization of the enormity of the task confronting the field collector who contemplates the possibility of examining the seemingly interminable lengths of the intestine of a whale, or even of a seal, under arctic conditions, the will to believe that nothing significantly new could be expected is readily understandable.

Recent Field Studies.—As a later development of an actual program, the staff of the Institute of Parasitology of McGill University at MacDonald College, in Quebec, began an extended survey of parasites of the far north under the direction of T. W. M. Cameron. With cooperation of other agencies they made extensive surveys of the parasites of sledge dogs, seals, and one species of whale from the St. Lawrence northward beyond the Arctic Circle, especially on Ellesmere Island and Baffin Island. All of the Acanthocephala from this series of surveys were made available to the present writer for critical study. Only preliminary reports were published by the Canadian colleagues (Cameron, Parnell,

and Lyster, 1940; and Lyster, 1940). Since this was the first extensive collection from marine mammals of the American Arctic, the series has special interest.

A report published by Cameron, Parnell, and Lyster (1940) was confined to a survey of the helminth parasites of sledge dogs. In it a single species of Acanthocephala was mentioned, *Corynosoma semerme*, which the present writer had identified for Professor Cameron. A more extensive paper by Lyster (1940) summarized the results of a series of expeditions and cooperative studies on the parasites of sea mammals conducted by and under the direction of the Institute of Parasitology. In that report only two species of Acanthocephala were mentioned and these were identified as *C. semerme* and *C. strumosum*. Some of that material has been available in the present study. The specimens which Lyster (1940:405) recorded as *C. strumosum*, common in the white whale (*Delphinapterus leucas*) in the Gulf of St. Lawrence, are here recognized as basis for description of a distinct species, *C. cameroni*. *C. strumosum* and *C. semerme* were both reported from the bearded seal (*Erignathus barbatus*) but both of Lyster's identifications are in doubt. In his description of *C. strumosum* from this host the measurements of the proboscis and its hooks exceed those of *strumosum*, as interpreted by the present writer, and agree more nearly with those distinctive of *C. hadweni*, which is described in the present contribution. Apparently due to a typographical error, the length of the embryos for this species is given as 1.080 mm by Lyster. Doubtless this was intended for 0.108 mm and this dimension is consistent with embryos of *C. hadweni*, not those of *C. strumosum*.

Specimens from the bearded seal (*Erignathus barbatus*) which Lyster identified as *C. semerme*, on the basis of comparison with specimens from the sledge dog identified by the present writer, are not in agreement with the series of specimens of *C. semerme* available in the present study. Through the courtesy of Professor Cameron, the writer has been accorded the privilege of examining some of these specimens and finds that they belong to the previously unrecognized species which is described in this paper under the name *C. validum*.

Very recently, a group of scientists from the United States has been operating in Alaska, making very extensive parasite surveys. This group includes Robert L. Rausch, R. B. Williams, E. L. Schiller, and B. Babero. Through phenomenal industry they have brought together the largest, most representative, and best prepared series of collections from marine mammals that have ever come out of the far north of America. In their surveys they have included other types of hosts which provide evidences of accidental extension of host relationships of the parasites of the seals and other marine mammals. Their spirit of cooperation has been in large

measure responsible for the comprehensive coverage of this portion of the present report.

In the literature, up to 1952, there is a record of only one species of Acanthocephala from marine mammals of North America which seems to be restricted to this continent. This concerns *Corynosoma obtusens* which Lincicome described in 1943 from California sea lion (*Zalophus californianus*). In the present report the immature stage of this species is recorded from marine fishes of the Pacific.

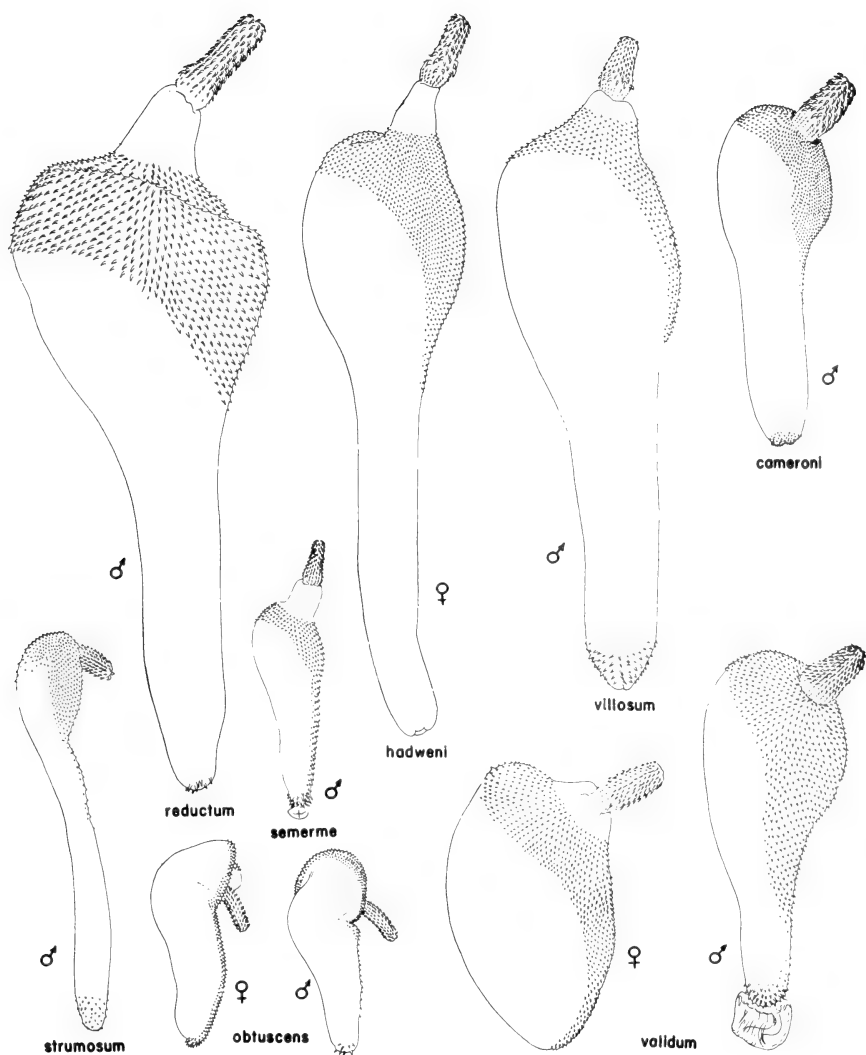
This rapid survey supports the earlier statement that the literature on the Palaeacanthocephala of North American mammals has been scant and scattered. It therefore forms a suitable background against which the details of the present report may be presented.

XI. ANALYSIS OF THE GENUS CORYNOSOMA IN NORTH AMERICAN MAMMALS

Diagnosis of Corynosoma.—With the characters of the subfamily Polymorphinae. Body length from 2 to about 10 mm; body club-shaped, thickened anteriorly as an inflated bulb or a flattened disc and usually with a narrow, cylindrical hind-trunk. Trunk spines (Text Fig. D) at least on the anterior extremity of the fore-trunk, extending farther along the ventral than on the dorsal surface, usually reaching into and at times extending the full length of the hind-trunk. Spines of variable forms, often sigmoidal, the tip of each commonly invested by a fold of the cuticula. Genital spines on the surface of the tip of the hind-trunk in the vicinity of the genital aperture may be present in both sexes or in one only, often obscured by introversion of the posterior extremity to form the genital vestibule. Neck usually short, in the form of a truncated cone. Proboscis usually directed somewhat ventrally away from the main body axis, commonly with an enlargement usually near to or posterior to its middle. Proboscis hooks (Text Fig. E) arranged in longitudinal rows, increasing in thickness of individual hooks from the anterior tip posteriorly, often with one or a few greatly enlarged hooks at or near the region of maximum diameter of the proboscis; basal series of one to six small thorns in each longitudinal row without reflected roots; other hooks each with an unbranched, reflected root, often longer than the length of the thorn. Proboscis receptacle a closed, double-walled muscular sac with the brain some distance anterior to its posterior extremity. Lemnisci usually shorter than receptacle, relatively broad, lateral edges often rolled. The male reproductive organs either restricted to the cavity of the hind-trunk or extending into the bulb of the fore-trunk. Testes rounded or slightly elongated, often somewhat overlapping. Six cement glands, pyriform to clavate. Mature embryos within body of a gravid female with a relatively short axial prolongation of the inner membranes at each pole. Distributed through all continents, associated especially with aquatic habitats. Aquatic mammals and water birds the normal definitive hosts, fishes the second intermediate host, and crustaceans the first intermediate host.

Type species, by original designation, *Corynosoma strumosum* (Rudolphi, 1802).

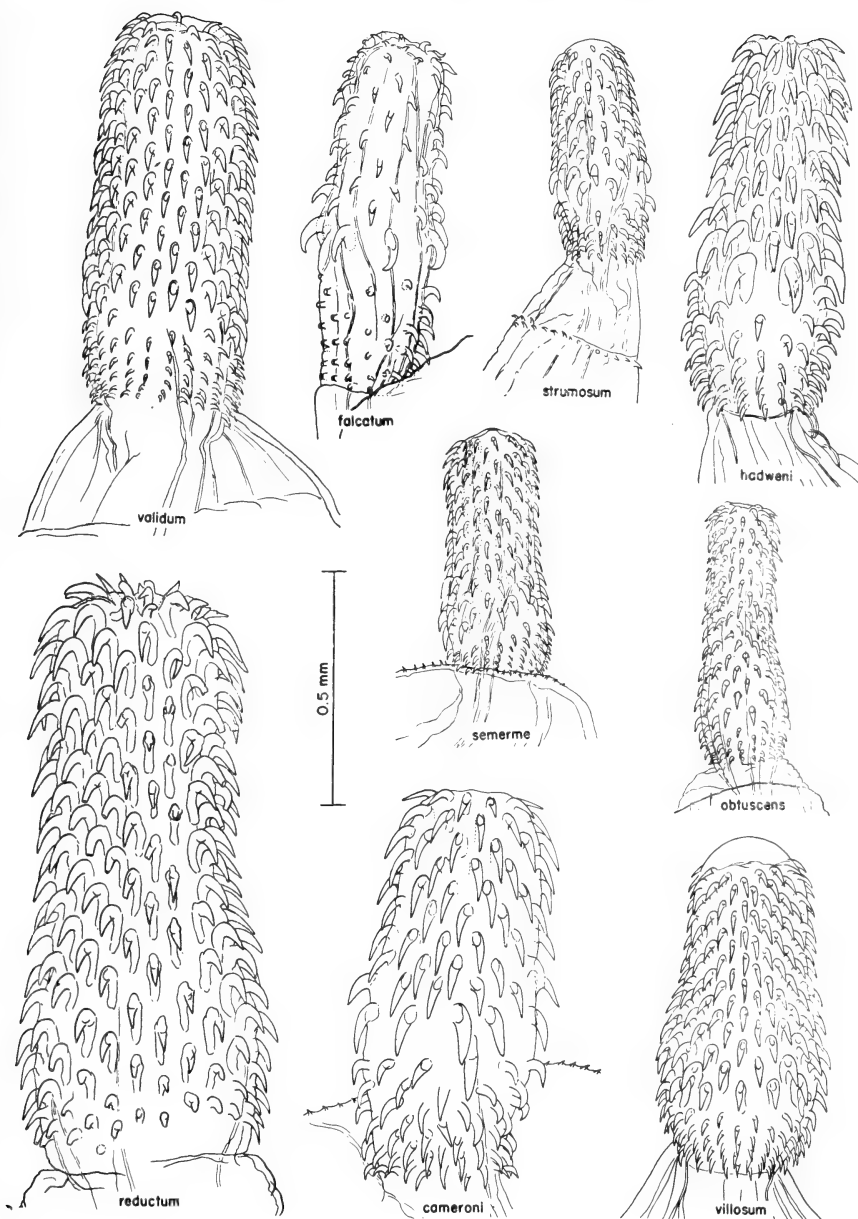
Host Relations.—Except for accidental introduction into unusual hosts,



TEXT FIG. D. External features of eight of the nine species of *Corynosoma* encountered in mammals of North America. All drawings at identical magnification. In instances of conspicuous dimorphism both sexes are illustrated. Drawings prepared by Charles A. McLaughlin, scientific artist in the Department of Zoology, University of Illinois. After Van Cleave, 1953.

most of the genera of Acanthocephala living in the intestine of warm-blooded vertebrates are distinctively the parasites of either birds or mammals. The genus *Corynosoma* is an exception to this rule, since both aquatic birds and mammals serve as normal definitive hosts to adult worms of this genus. While the literature is full of references to the occurrence of the same species of *Corynosoma* in birds as well as mammals, there is a growing body of evidence which indicates that each species is distinctively restricted to one or the other of these as normal hosts. Individuals which accidentally get into the intestine of a member of the other group are often unable to reach full sexual maturity. As early as 1905, Forssell discovered that specimens of *Corynosoma strumosum* and of *C. semerme*, both of which are characteristic parasites of seals, may occur in fish-eating birds. However, according to his extended observations, they never reach functional maturity in birds. Furthermore, his attempts at experimental infection of birds by these same species of *Corynosoma* supported his conclusion. More recently, Lundström (1942) has reiterated the same conclusion based upon his studies of natural infections by *Corynosoma* in Swedish hosts.

Body Spines.—Members of the genus *Corynosoma* are the only Acanthocephala of the warm blooded vertebrates which characteristically have cuticular spines on the fore part of the trunk and also around the genital extremity (Text Fig. D). Unfortunately, the genital spines, one of the most significant of the generic characteristics, are not always observable. In many individuals they are originally present but secondarily become either lost or concealed in the performance of normal bodily functions; in some species they are normally present on individuals of one sex but are lacking on the other; and in still other species commonly regarded as belonging to *Corynosoma* they are apparently entirely wanting. The present writer (Van Cleave, 1920) showed that in at least some females of this genus the genital spines adhere so firmly to the cement substance of the copulatory cap that they are torn loose from the body when the cap is shed. For a long time this mutilation was thought to represent a distinctive type of sexual dimorphism. In still a later paper (Van Cleave, 1945b) it was demonstrated (Fig. 50) that in some species of *Corynosoma* introversion of the posterior extremity of the trunk displaces the genital spines from their customary position on the surface of the body and conveys them to a position within the posterior end of the trunk in a chamber which has been designated as the genital vestibule. Under most circumstances, the genital spines within the genital vestibule are not observable in whole mounts. In one species, *C. mergi*, dimorphism is regarded as normal by Lundström (1941, 1942) who maintains that the females of this species possess genital spines although genital spines are lacking in males. There are a number of additional species



TEXT FIG. E. Proboscides of the nine species of the genus *Corynosoma* from North American mammals, all drawn to identical magnification for immediate comparison of proboscis size and shape and for details of form and arrangement of the hooks.

which have been assigned to *Corynosoma* even though no evidence of genital spines has been found. Some of these are doubtless forms in which the genital spines are withdrawn into the genital vestibule. Perhaps some species have been incorrectly ascribed to the genus *Corynosoma* and should be transferred to either the genus *Arhythmorhynchus* or to *Polymorphus*, both of which have many points in common with *Corynosoma* but differ particularly from that genus in that neither of them ever has genital spines and the proboscis is usually of a distinctly different shape, especially in *Polymorphus*. All of the species of *Polymorphus* and *Arhythmorhynchus* are parasites of birds with no species occurring characteristically in mammals. Instances of accidental occurrence in mammals are much less frequent than for *Corynosoma*. Before the significance of the genital vestibule as a morphological feature destroying the external evidence of genital spines was understood, the present writer (Van Cleave, 1934) called attention to the unsatisfactory basis for distinguishing between *Corynosoma* and several other genera of *Acanthocephala*, chiefly from birds. Gradually these obstacles have been overcome by the discovery of additional morphological distinctions to support the original generic characterizations and in part by recognizing that some presumed genera must be regarded as synonyms of others.

Arrangement of Trunk Spines.—The distribution of trunk spines furnishes some readily available criteria for the differentiation or at least the grouping of species of *Corynosoma*. Almost invariably the spines are definitely restricted in their distribution. Regardless of the pattern of their distribution, they extend farther posteriorly along the ventral surface than on the dorsal (Text Fig. D). This is in keeping with the fact that the attached worm lies with the ventral surface in contact with the host intestinal wall and thereby the ventral spines serve as a secondary means (Van Cleave, 1952b) of keeping the body of the parasite in intimate contact with the mucosa of the host.

Frequently the spines of the trunk are arranged in distinctive geometrical pattern. The tip of each spine is often invested in a slight triangular elevation of the cuticula so that a fold of the cuticula slants away from each spine tip, giving to the body surface a semblance of diamond-shaped surface markings. Several authors (especially von Linstow, 1905) have overemphasized this surface pattern in their portrayal of the spines, stressing the surface meshwork but omitting the spines which impose the pattern.

For a long time *Corynosoma strumosum* and *C. semerme* were the only widely known representatives of the genus. During that time it became a common practice to regard the distinctive difference in trunk spination shown by these two species as specific. In *C. semerme*, the

trunk spines extend uninterruptedly along the entire ventral surface so that those of the genital area merge directly with the other spines. In contrast, there is a distinct gap between the trunk spines and genital spines of *C. strumosum*. This means of differentiation is so easily applied that it came to be regarded as available for separating immature individuals of the two species even when proboscis characters could not be observed. Later, with the discovery of additional representatives of the genus, this simple basis for specific identification became invalidated. Thus, for example, Lincicome (1943) discovered that in females of *C. obtuscens* the trunk spination along the ventral surface (Fig. 37) is continuous with the genital spines, similar to conditions found in both sexes of *C. semerme*, but the males of *C. obtuscens* have a bare area (Fig. 38) between the trunk spines and those of the genital area, similar to conditions found in both sexes of *C. strumosum*.

In *C. validum* from the walrus, a species which is described later in this monograph, the trunk spines extend along almost the entire length of the ventral surface of the oddly shaped body of the female, while in the male much of the cylindrical hind-trunk is devoid of spination.

Lundström (1941) found that in *C. mergi* the anterior spine field is divided into two distinct bands encircling the front end of the trunk with a non-spined zone between the two bands. A similar condition has been recorded for a species of *Arhythmorhynchus* (Chandler, 1935).

The simplest modification of the spine-clad anterior extremity of the trunk in *Corynosoma* is an enlargement or inflation of that part of the body. However, in some species of this genus the neck retractor muscles cause the neck and a portion of the trunk to become withdrawn into a crater-like depression which carries the proboscis in its center. This produces a distinctive body shape which is often referred to in the literature as similar to a large-bowled pipe with the attenuated posterior region representing the stem. As the crater is formed by retraction of the base of the proboscis, a fold of host tissue becomes wedged between the base of the proboscis and the introverted, spine-clad, trunk crater where it is held tenaciously by the combined action of proboscis hooks and body spines acting on the two opposite surfaces of the fold of host tissue.

Transitional Species.—The ease with which the gap between *Corynosoma* and *Polymorphus* seems to be bridged is well demonstrated in the perplexities of Skrjabin (1913) and of Travassos (1915b). Skrjabin, working in Turkistan discovered a new species which he thought was intermediate between the two genera. To it he ascribed the name *Polymorphus corynoides* with the expressed intention of thus commemorating the fact that the species has characteristics of both of these genera. He further expressed the belief that subsequently the development of the

taxonomy of the Acanthocephala might result in the recognition of a distinct genus intermediate between *Polymorphus* and *Corynosoma* to accommodate his *P. corynoides*. If there were a consistently intermediate group of species with clearly marked distinctive features between the limits of the two genera, the recognition of a third genus might seem tenable. However, when the intermediate forms show no such agreement among themselves, the recognition of another genus would but multiply the difficulties. Instead of there being the necessity for establishing a single line to distinguish between *Polymorphus* and *Corynosoma*, it would then become imperative to erect two lines of cleavage, one to separate the intermediate group from *Corynosoma* on the one side and another to separate the new group from *Polymorphus*.

Travassos (1915b) discovered in the Brazilian fauna a new species which he named *Polymorphus caryosoma*. In spite of the error in spelling the species name, Travassos made it clear in his paper that the name was chosen to give testimony to the presence of features resembling those of *Corynosoma*. Similar problems involving lack of clear-cut evidences of generic relationships do not exist in the species infecting mammals of North America, hence the identity and generic assignment of the problematical forms will not be considered in the present paper. This contribution will cover the general historical background of the genus *Corynosoma* and its species and only those forms occurring in North American mammals will be considered in detail.

Normal Definitive Hosts.—In the North American fauna there is fairly sharp cleavage of the species of *Corynosoma* along lines of host relationships. In a few instances the writer has observed a mammalian *Corynosoma* in a bird and avian species in a mammal but this is a relatively rare occurrence. Thus, Rausch and Schiller have submitted to the writer a few specimens of *Corynosoma* from a bald eagle taken in Alaska. All of the specimens are immature and in every morphological feature are identical with specimens taken from seals of the same locality. There is little doubt but that fishes serve as second intermediate host in this instance and the immature worms entered the intestine of the eagle along with the fish host. There they became at least temporarily established although they probably could not produce viable eggs. In spite of the fact that the species of *Corynosoma* infecting birds of North America are specifically distinct from those inhabiting the intestine of mammals, no one has ever succeeded in detecting any morphological basis for sub-generic groupings of the species capable of setting off the species living in the intestine of birds from those occurring in mammals.

The host relationships of the members of the genus *Corynosoma* offer many fascinating problems for consideration. An examination of many thousands of specimens of *Corynosoma* from North American hosts has

yielded but a single indisputable instance of the occurrence of an avian species of *Corynosoma* in a mammalian host. On November 4-5, 1947, Dr. Robert Rausch found seven specimens of *C. constrictum* in two mink (*Mustela vison*) taken in Horicon Marsh, Wisconsin. This is distinctively an avian species of *Corynosoma* for which extensive field collections have shown that it is of common occurrence in water birds of that locality.

It appears that normal host limitation is probably attributable to some interrelationship between feeding habits of the definitive hosts and the kinds of animals utilized by the worms as intermediate hosts. It is well known that fishes act as reservoir hosts for several of the *Corynosoma* infecting mammals, such as *C. strumosum*, *C. semerme*, and *C. obtuscens*. Juvenile worms in fish reservoir hosts may be introduced with equal readiness into fish-eating birds or mammals. It seems probable that for the species restricted to birds as definitive hosts, reservoir intermediate hosts may be lacking. Under such conditions the aquatic bird would acquire its infection by feeding upon small crustaceans or other infected arthropods which would not ordinarily be eaten by mammals.

History of Corynosoma.—In the literature there has been much confusion and futile discussion as to the date for the concept and the name *Corynosoma*. Luehe (1904:231) named and briefly characterized the genus and cited *C. strumosum* as the type species. The date has been very generally misquoted as 1905, although some writers have completely overlooked the original article and have quoted 1911 as the date for this genus. The 1905 citation is due to the fact that Luehe's extensive historical treatment of the *Acanthocephala* appeared in two issues of the *Zoologische Annalen*, the parts of which, with directly continuous pagination, were published in 1904 and 1905, respectively. The section containing the proposal of *Corynosoma* as a new genus (page 231) was printed and distributed in 1904 as shown by the present writer (Van Cleave, 1945b:302) in a critical review of the evidence and discussion of the errors in citation. The definite establishment of the 1904 date for this genus solves the problem of priority between *Corynosoma* and the name *Chentrosoma* which Monticelli proposed in 1905. Travassos (1926:52) cited 1911 as date for *Corynosoma*. In 1907, Porta (page 412) had proposed the name *Echinosoma* for a heterogeneous assemblage of species of *acanthocephalans* and Meyer (1932) regarded this name as in part a synonym of *Corynosoma*. However, the name *Echinosoma* as used by Porta has no nomenclatorial standing. *Echinosoma* had previously been proposed as a generic designation in other groups by several different authors and hence could never be available for any concept in the *Acanthocephala*.

The extent of the preoccupation of *Echinosoma* is summarized by

F. E. Schulze *et al.* (1929) in volume 2 of his *Nomenclator animalium generum et subgenerum*, where he lists the following uses prior to the proposal by Porta: in 1839 by J. Audinet-Serville in Orthoptera, in 1854 by T. V. Wollaston in Coleoptera, in 1868 by C. Semper in Echinoderma, in 1881 by E. Girschner in Diptera, and in 1883 by A. Pomel in Echinoderma.

Recognizing Species.—Recognition of the species within the genus *Corynosoma* has been extremely difficult, chiefly because so many of the species have been inadequately and incorrectly described. Several of the nominal species are without doubt untenable but the extent of the synonymy is not readily determinable. The genus is world-wide in its geographical distribution. Lack of physical barriers to the dispersal of migratory water birds and marine mammals has greatly impeded any final solution to the problems of geographical distribution of members of the genus *Corynosoma*. Doubtless, claims of practically world-wide geographical distribution of some species are based upon erroneous identifications but similarly some species that have been regarded as distinct are in reality identical, even though they occur in different host species whose geographical ranges do not overlap. While specific life histories are unknown for most species of this genus, it is well demonstrated that many have broad host tolerances, especially as juvenile and larval stages infecting intermediate hosts. If suitable intermediate hosts are available, any internal parasite which gains access to the definitive host by way of ingested food may far exceed the geographical limitations of any single definitive host species. Some of the problems of identity and of synonymy are beyond any possibility of final conclusion at the present state of knowledge. In the European fauna, where all early basic knowledge of the Acanthocephala had its origin, most of the investigators and reviewers have failed to give any precise information on such essential features as hook and embryo measurements for even those species which are presumed to be common or familiar forms. Details as to the numbers and arrangement of the proboscis hooks are not available in many descriptions, while confusion in methods of expressing the hook formulas, actual errors in simple enumeration, utter inconsistency between text statements and conditions shown in drawings, and failure to indicate normal range of individual variability in hook formulas all combine to pyramid the difficulties of recognizing most of the species of *Corynosoma*. Consequently, since the presumably "well-known" forms of Europe are inadequately, incorrectly, and inconsistently described and differentiated, students of other countries have been unable to make satisfactory comparisons between forms of *Corynosoma* which they have encountered and the previously named species.

At the hands of the most recent competent reviewer (Meyer, 1931b),

three species of *Corynosoma* are recorded for the Arctic realm. To the commonly recognized *C. strumosum* and *C. semerme*, he added a species of doubtful status, *C. reductum* (von Linstow, 1905) which was based on immature individuals. All three of these species were recorded by Meyer from the Eurasian continent and adjacent islands with no mention of occurrence on the American continent, although the two common species were recorded from Greenland. Except for a very few references, the North American representatives of the genus *Corynosoma* are very imperfectly known. So far as the Arctic realm of this continent is concerned, the genus *Corynosoma* has remained practically untouched down to very recent times. When the United States came into possession of the Alaskan territory, extensive investigations of the biological resources were undertaken. Because of their great economic importance, the fur seals were made the object of particular study. David Starr Jordan and a staff of investigators studied the diseases and parasites of the fur seals but in their reports (Stiles and Hassall, 1899) they made no mention of encountering *Acanthocephala* in the fur seals and in the subsequent literature there has been no record for this host. For a long time this absence of references to *Acanthocephala* in fur seals was taken as evidence that these animals might be immune to infection by *Corynosoma*, in spite of the fact that other marine mammals of the Pribilof Islands were known to be infected.

Finally, through the courtesy of Victor B. Scheffer and J. E. Lynch a collection which the former took from fur seals became available for study. In his inimitable technic, Dr. Lynch stained and mounted the specimens and turned the slides over to the writer for study. In a relatively small collection three different species of *Corynosoma* (*C. strumosum*, *C. semerme*, and *C. villosum*) were recognized, thus dismissing the myth of a possible immunity of fur seals to *acanthocephalan* infection.

When attempts at identification of many of the collections from North America have been assayed, they have often proved extremely difficult because of the glaring misinformation which has passed currently for several of the species from other continents. Most of the conservative students who have studied the *Corynosoma* from mammals of North Atlantic of Europe have commonly assumed that but two species are represented in that faunal area. Rarely is this assumption supported by detailed descriptions of specific morphological characters. More often, the obvious difference in body spination alone is mentioned. Of the two common European species, *C. semerme* has the body spination continuous along the ventral surface while *C. strumosum* has a broad unspined zone separating the spine field of the anterior part of the trunk from the genital spines at the posterior tip of the body. This basis for comparison and contrast has been particularly useful in studies of immature

specimens, especially juvenile worms carried by a second intermediate host. All too often these juveniles have the proboscis completely introverted. Within a well-known faunal area, field characters such as these are very useful and convenient. However, significant difficulties arise when the student attempts to discover how far away from northern Europe the obvious external body differences, unsupported by more subtle morphological characters such as details of proboscis armature, may stand alone as safe criteria for differentiation of species. Thus, for example, on the basis of body spination the North American fauna includes "semerme-like" and "strumosum-like" *Corynosoma* and parallel groups of species exist in the Antarctic. For these it is wholly unsafe to assume either identity with or distinctness from the corresponding European species until full details of morphology are available for contrast and comparison. Unfortunately, even some of the most reliable of the European investigators have completely ignored detailed measurements of hooks for *C. strumosum* and *C. semerme*. Luehe (1911) gave no information on hook sizes for these species. In his impressive monograph, Meyer (1932) has cited no measurements of either hooks or embryos for either of the two common European species. For one species of the genus he did show (Meyer, 1932, fig. 55) that the size and appearance of the individual egg change markedly during its development within the body of the female worm.

Lack of Barriers for Corynosoma.—In the past it has been often assumed that wide separation of two areas furnishes sufficient evidence of the distinctness of the species of *Corynosoma* encountered in the respective regions. When migratory and far ranging hosts are concerned this assumption is untenable. This is particularly true in the polar regions where it has been shown (Van Cleave and Lynch, 1950; Van Cleave and Rausch, 1951) that many of the usual barriers to distribution of Acanthocephala are not operative. This fact is attributable in large measure to the widespread and continuous distribution of various species of potential larval and second intermediate hosts and suitable definitive hosts under fairly uniform ecological conditions. Wide dispersal of intestinal parasites under these circumstances does not necessarily involve extensive migratory movements of the individual definitive host. Although wide ranging movements of any given species of definitive host are not essential for the distribution and maintenance of territory of the parasite, migration may support the other factors mentioned above. Under these circumstances, host specificity or limitation for any given species of *Corynosoma* in polar seas depends largely upon restricted and distinctive food habits of the natural definitive host being essentially different from those of other potential hosts occupying the same territory.

The lack of definite physiographical barriers to the geographical dis-

tribution of definitive hosts of some species of *Corynosoma*, such as the seals, sea lions, and other marine mammals, and most of the aquatic birds, adds complication to the problem of circumscribing and differentiating the species of their parasites. Biologically, it is unsound to assume that the geographical distribution of a species of *Corynosoma* is coextensive with the range of its common mammalian or avian host animal. It is just as indefensible to assume that distribution of the parasite is limited by the distribution of its known definitive hosts. Many species of *Acanthocephala* utilize different definitive hosts in different regions, while on the other hand the definitive host may be free from a given species of parasite in part of its range because suitable intermediate hosts are not available to perpetuate the infection. The universal inclusion of a wide variety of both arthropods and fish in the diet of practically all aquatic birds and mammals renders a large number of vertebrates potential hosts for *Corynosoma* species. The lack of critical specific identifications and uncertainty of the status of most of the immature worms found in intermediate hosts renders many of the older records of the occurrence of *Corynosoma* unintelligible, even in areas where field studies have been carried on for several generations. The abundance of seals and other fish-eating mammals and birds in the Arctic and Antarctic sea presents unusually favorable conditions for the establishing of *Corynosoma* in these regions. However, most of the records from the Arctic and the Antarctic regions are based upon fortuitous discoveries by exploring parties which are made under conditions prohibiting detailed studies of seasonal distribution and development and physiological adaptations to host species. Consequently, some of the most confused literature relating to the genus *Corynosoma* pertains to the published results of exploring expeditions. This confusion is further traceable to the fact that scientists who are chosen for writing the reports on parasitic worms are often wholly unfamiliar with the literature on *Acanthocephala* and know nothing of the extent of individual variability in members of this phylum.

Common Sense Segregation of Materials.—As the present study of the literature and of collections of *Corynosoma* proceeded, it became obvious that the confusion of species existing in the literature does not extend to the collections of actual specimens. In the course of this study the writer became convinced that in a truly representative series of collections the individual species of *Corynosoma* could be distinguished and separated with a considerable degree of certainty on the basis of external features. Conformity in general body shape, size, and proportions; shape, size, and position of the proboscis; and distribution of the trunk spines and their relations with the genital spines offer a complex of differences and likenesses readily available for preliminary grouping and segregating specimens before delving into the specific details of proboscis hook formulae

and minute micrometric measurements of bodily dimensions, hooks, spines, and embryos. Preliminary macroscopic evaluation of hundreds of microscopic mounts proved so satisfactory for preliminary grouping of the material that but few changes had to be made when more minute morphological features were taken into consideration. Very commonly the specimens misjudged on general external features were either young individuals which had not as yet attained definitive body form or were specimens that had been improperly treated before or during the procedures of killing and fixing.

The high degree of success attending the preliminary attempts at grouping and separating the species on gross external features was so gratifying that a decision was reached to introduce this method for differentiating the species before presenting the finer morphological details on which the specific taxonomy ultimately rests.

To this end a series of "habitus" drawings, omitting all internal details, was prepared (Text Fig. D) to show the external features of eight of the nine species of *Corynosoma* treated in this monograph. The ninth species, *C. falcatum*, is readily distinguishable (Text Fig. E) on the basis of the proboscis and its hooks. Furthermore, some shrinkage of the body wall and relatively dense internal structures precluded the possibility of determining the exact arrangement of the trunk spines in the small number of individuals of *C. falcatum* that were available for study.

Mr. Charles A. McLaughlin, scientific artist in the Department of Zoology of the University of Illinois, prepared, under direction, the series of semi-diagrammatic drawings that are here shown as Text Fig. D. The entire series is at uniform magnification and all drawings are of characteristic, mature individuals. Consequently comparisons may be made directly from one drawing to another. Where conspicuous sexual dimorphism is present both sexes are shown in this series of drawings.

To supplement the general anatomical features shown in Text Fig. D, Text Fig. E shows the intimate details of proboscis size and shape and the relative size, number, and arrangement of the proboscis hooks for each of the nine species of *Corynosoma* treated in the present monograph. Here again all drawings were made at identical magnification so that direct comparisons can be made. The originals of these drawings were prepared by Mrs. Katharine Hill Paul, scientific artist, now retired, in the Department of Zoology of the University of Illinois.

Descriptions of Species of Corynosoma.—

***Corynosoma strumosum* (Rudolphi, 1802)**

(Text Figs. D and E; Plate 1, Figs. 1 to 15)

Synonyms: *Echinorhynchus strumosus* Rudolphi, 1802, of various authors.
Echinorhynchus hystrix Bremser, 1824, of various authors, in part.
Echinorhynchus ventricosus Rudolphi, 1809.

Echinorhynchus gibbosus Rudolphi, 1809, in part.

Echinorhynchus striatus of Villot, 1876, *nec* Goeza, 1782.

Echinorhynchus gibber Olsson, 1893, in part.

Corynosoma osmeri Fujita, 1921.

Corynosoma ambispinigerum Harada, 1935.

?*Echinorhynchus incrassatus* of Linton, 1891, *nec* Molin, 1829.

?*Echinorhynchus carchariae* Linton, 1891.

MATERIAL.—In the present study considerably more than two hundred specimens of *C. strumosum* have been studied critically and compared with specimens from European collections. The type material has not been available.

DIAGNOSIS.—Bodies of two sexes not conspicuously different in size and shape, narrowly attenuated, commonly 5 to 7 mm long, occasionally reaching 9 mm. Inflated fore-trunk about one-fourth to one-third the length of entire trunk, usually in form of an elongated ellipsoidal swelling, rarely set off as a distinctly flattened disc, often bent somewhat ventrally with the dorsal surface more prominently inflated than the ventral. Hind-trunk conspicuously narrower than fore-trunk and about twice its length, with but little variation in diameter through its length except that it becomes somewhat narrowed in the region of the genital opening, especially in the male. Fore-trunk with a dorso-ventral diameter often reaching 1 mm, hind-trunk considerably less than half this diameter. Trunk spines (0.022 to 0.050 mm long) fairly uniformly dispersed over the fore-trunk and along the ventral surface extending on the hind-trunk about half its length; appearing again as genital spines around the posterior extremity, especially of males, but often introverted into the genital vestibule and therefore not observable from the surface. Genital spines 0.022 to 0.028 by 0.008 to 0.011 mm, not in perfect rows but commonly about 6 or 8 are recognizable in a longitudinal series. Some females show scattered genital spines, less numerous than in males, although some or all of these may be removed when the copulatory cap is shed.

Neck short, a truncated cone, in preserved specimens often retracted into the fore-trunk as a fold surrounding the base of the proboscis. Proboscis approximately cylindrical with a swollen band at the region between the middle and basal thirds of the length, narrowed somewhat at base; length 0.50 to 0.69 mm, maximum diameter 0.20 to 0.25 mm; armed with usually 18 longitudinal rows of 10 or 11 hooks each, of which the anterior 5 or 6 (occasionally 7) of each row are provided with strongly recurved roots while the basal 4 of each row are devoid of prominent roots and are closely crowded together. The posterior hook of each of the rooted series, located on or near the level of the greatest diameter of the proboscis, is considerably heavier than any of the others, 0.064 to 0.080 mm long with a diameter of 0.026 to 0.032 mm at the bend where thorn and root unite; its root longer than the projecting thorn. Anterior to the

heaviest hook in each longitudinal row the hooks progressively decrease in diameter, in some instances they become less recurved toward the anterior extremity of the proboscis and some may have straighter and slightly longer thorns than the heavier hooks. Small basal hooks often strongly crescentic in shape or at times sharply angular, about 0.032 to 0.040 mm, as a straight line measurement from tip to base.

Lemnisci broad and flat, shorter than the proboscis receptacle. Male organs located in the anterior region of the cylindrical part of the hind-trunk. Subspherical testes in contact and contiguous with the six pyriform to clavate cement glands.

Embryos in body of female about 0.079 to 0.101 by 0.019 mm, with small, rounded outpocketing at each pole.

First intermediate host unknown but almost certainly an arthropod and probably an amphipod.

Second intermediate hosts in America: infective larvae encysted in liver and other viscera of marine fishes of the Pacific coast of northwestern United States and of Canada, with the following definitely demonstrated as hosts: *Platichthys stellatus*, *Lepidopsetta bilineata*, *Leptocottus armatus*, and *Gadus macrocephalus*. Under the misidentification as *C. osmeri*, Ward and Winter (1952) record the removal of immature *C. strumosum* from the mesenteries of *Umbrina roncadore*, the yellowfin croaker, of Catalina Island, California.

Definitive hosts in America: California, the harbor seal (*Phoca vitulina richardii*) and the California sea lion (*Zalophus californianus*); Alaska and the Arctic, the grey seal (*Halichoerus grypus*), the ringed seal (*Phoca hispida*), bearded seal (*Erignathus barbatus*), harbor seal (*Phoca vitulina*), and unidentified "seals" of Alaska and the Arctic of North America.

ACCIDENTAL INFECTIONS.—Dr. Rausch and Dr. Schiller each secured a single immature specimen of *C. strumosum* from the bald eagle (*Haliaeetus leucocephalus*) of Alaska. There is little doubt that both of these instances represent temporary accidental infections obtained when the eagles fed upon infected fishes serving the parasite as second intermediate host. It is also possible that the following hosts, listed in the host tabulation, are likewise accidental infections; the sea otter (*Enhydra lutris*) and the domestic dog (*Canis familiaris*) from Alaska, and an undetermined variety of the mink (*Mustela vison* var.?) from Oregon.

ERRONEOUS IDENTIFICATIONS.—Specimens of *Corynosoma* from the white whale (*Delphinapterus leucas*) which Lyster (1940) identified as *C. strumosum* have been re-examined (Van Cleave, 1953) and made the basis for a distinct species, *C. cameroni*. Furthermore, the description and figures of *C. strumosum* which Lyster identified from the bearded seal

(*Erignathus barbatus*) seem to apply to the species which is herein regarded as *C. hadweni*, and are not *C. strumosum*.

In Europe the following additional definitive hosts have been named in the literature, the Greenland seal (*Phoca groenlandica*) and the hooded seal (*Cystophora cristata*). Furthermore, a long list of aquatic birds has been named as definitive hosts for this species but the evidence seems to indicate that none of these is a normal host, since none is able to bring the worms to functional maturity.

A considerable number of fishes has been recorded for Europe as carrying larvae of *C. strumosum*. In the following list the names of fishes given by European workers are quoted directly without verification of validity of the name of the genus or species: *Clupea harengus*, *Conger conger*, *Cottus quadricornis*, *C. scorpius*, *Cyclopterus lumpus*, *Gadus callarias*, *Gasterosteus aculeatus*, *Lophius piscatorius*, *Lota vulgaris*, *Osmerus eperlanus*, *Perca fluviatilis*, *Pleuronectes flesus*, *P. limanda*, *Rhombus maximus*, *Trachinus draco*, *Zoarces viviparus*, *Myxocephalus quadricornis*, *Coregonus laveratus*, *C. fera*.

In Japan, under the names of *Corynosoma ambispinigerum* and *C. osmeri*, what seems to be *C. strumosum* has been recorded from an undetermined species of *Phoca* and also, as larval stages, in second intermediate hosts *Sciaena schlegeli* and *Osmerus lanceolatus*.

RECORDS OF OCCURRENCE OF *C. strumosum*.—

Host	Locality	Date	Collector	Accession number
<i>Halichoerus grypus</i>	Unalaska, Al.	Dec. 4, 1920	Hadwen	VC 1932
<i>Halichoerus grypus</i>	Unalaska, Al.	Dec. 4, 1920	Hadwen	VC 2637
<i>Halichoerus grypus</i>	Unalaska, Al.	Jan. 21, 1921	Hadwen	VC 1933
<i>Phoca hispida</i>	Point Barrow, Al.	Apr., 1949	Rausch	VC 4268
<i>Phoca hispida</i>	Point Barrow, Al.	Apr., 1949	Rausch	VC 4269
<i>Phoca hispida</i>	Point Barrow, Al.	May 5, 1949	Rausch	VC 4311
<i>Phoca hispida</i>	Point Barrow, Al.	May 13, 1949	Rausch	VC 4310
<i>Phoca hispida</i>	Point Barrow, Al.	Apr. 19, 1949	Rausch	VC 4353
<i>Phoca hispida</i>	Point Barrow, Al.	Oct. 1, 1949	Rausch	VC 4435
<i>Callorhinus alascanus</i>	Pribilof I.	?	Scheffer	VC 3991
<i>Phoca vitulina richardii</i>	Ventura Co., Cal.	May 27, 1928	Ball
<i>Phoca vitulina richardii</i>	Kodiak I., Al.	1940	Morton	VC 3992
<i>Phoca vitulina</i>	Amchitka I., Al.	Mar. 10, 1952	Rausch	VC 4624
<i>Phoca</i> sp.	Kotzebue, Al.	May 2, 1949	Rausch	VC 4352
<i>Phoca</i> sp.	Aniakleet, Al.	May 5, 1949	Rausch	VC 4354
"Seal"	St. Lawrence I., Al.	Apr. 27, 1950	Rausch	VC 4427
"Seal"	St. Lawrence I., Al.	Apr. 28, 1950	Rausch	VC 4430
"Seal"	St. Lawrence I., Al.	May 1, 1950	Rausch	VC 4431
"Seal"	St. Lawrence I., Al.	May 1, 1950	Rausch	VC 4432
"Spotted seal"	St. Lawrence I., Al.	Aug., 1950	Schiller	VC 4450
"Spotted seal"	St. Lawrence I., Al.	Aug., 1950	Schiller	VC 4451
<i>Zalophus californianus</i>	Ventura Co., Cal.	1941?	Herman	VC 3590
<i>Enhydra lutris</i>	Amchitka I., Al.	1950	Rausch	VC 4516
Dog	St. Lawrence I., Al.	Apr., 1951	Schiller	VC 4506
<i>Mustela vison</i>	Corvallis, Ore.	Nov. 11, 1937	Shaw	VC 3120
<i>Mustela vison</i>	Corvallis, Ore.	?	Shaw	VC 2466

Larval stages

<i>Host</i>	<i>Locality</i>	<i>Date</i>	<i>Collector</i>	<i>Accession number</i>
<i>Platichthys stellatus</i>	Puget Sound, Wash.	1941-42	Lynch	VC 3993
<i>Leptocottus armatus</i>	Puget Sound, Wash.	1941	Lynch	VC 3994
<i>Gadus macrocephalus</i>	Puget Sound, Wash.	1941	Lynch	VC 3995
<i>Umbrina roncadore</i>	Catalina I., Cal.	July, 1949	Ward and Winter

***Corynosoma semerme* (Forssell, 1904)**

(Text Figs. D and E; Plate 2, Figs. 17 to 28)

Synonyms: *Echinorhynchus semermis* Forssell, 1904.*Echinorhynchus strumosus* Rudolphi, 1802, of various authors, in part.*Echinorhynchus hystrix* Bremser, 1824, of various authors, in part.*Echinorhynchus gibber* Olsson, 1893, in part.

MATERIAL.—In the present study 70 specimens of *C. semerme* from North American hosts have been studied and compared with individuals from northern Europe. While the types have not been available, the collection of the writer contains six specimens from Finland which had been identified by A. L. Forssell, author of the species. These were obtained by exchange from the Helsingfors Museum through the courtesy of K. M. Levander.

DIAGNOSIS.—Body small but thickset. The fore-trunk either enlarged as an ellipsoidal swelling or flattened ventrally as a disc. Hind-trunk short, usually not as long as the fore-trunk from which it is not conspicuously set off. Instead of the hind-trunk having a cylindrical shape, as in many species of the genus, it often tapers gradually toward the genital extremity. Bodies of the two sexes not conspicuously different in size or form, usually about 3 mm long and from 0.7 to 1.0 mm in maximum dorso-ventral diameter, gradually reducing to less than one-half that diameter near the posterior extremity. Trunk spines distributed over the anterior part of the fore-trunk and extending ventrally along the entire length of the hind-trunk, becoming directly continuous with the genital spination. Each ventral spine often emerging from a slightly elevated rounded papilla. Spines usually sigmoidal in shape, those at the genital extremity about 0.035 to 0.53 mm in length by 0.011 to 0.014 mm in width.

Neck short, not prominent, often retracted as a fold within the fore-trunk, surrounding the base of the proboscis. Proboscis nearly cylindrical, with but slight enlargement at the anterior end of the basal third, its length from 0.5 to 0.6 mm and its diameter from 0.2 to 0.3 mm. Usually the proboscis is directed ventrally from the ventrally curved anterior extremity of the fore-trunk, the angle of its incidence with the body axis depending on conditions at time of fixation. Proboscis armed with 22 to 24 longitudinal rows of 12 or 13 hooks each, clearly distinguish-

able as a series of 7 to 9 anterior hooks with recurved roots and a contrasting series of 4 or 5 small, closely crowded thorns at the base of each row lacking recurved roots. Roots of anterior hooks commonly about the same length as or longer than the corresponding thorn. The anterior hooks becoming progressively heavier from the tip posteriorly where the last large hook in each row is about 0.067 mm long and has a diameter of about 0.022 mm at the bend where the thorn merges into the root.

Spheroidal testes in contact or overlapping one another, reaching anteriorly beyond the posterior level of the proboscis receptacle and followed by six pyriform cement glands, arranged approximately in pairs.

Embryos within the body cavity of gravid females 0.079 to 0.101 mm long by 0.016 to 0.029 mm in width, with a rounded prolongation of one of the membranes at each pole.

First intermediate host unknown for America. In Europe (Nybelin, 1924), an amphipod (*Pontoporeia affinis*).

Second intermediate hosts unknown for America. In Europe, numerous fishes including *Acerina cernua*, *Cottus quadricornis*, *C. scorpius*, *Rhombus maximus*, *Pleuronectes flesus*, *P. limanda*, *P. platessa*, *Osmerus eperlanus*, *Clupea harengus membras*, *Anguilla anguilla*, *Blicca bjoerkna*, *Coregonus albula*, *C. fera*, *Cyclopterus lumpus*, *Gadus callarias*, *Lota vulgaris*, *Onos cimbrius*, *Perca fluviatilis*, *Zoarces viviparus*.

Definitive hosts in America: the bearded seal (*Erignathus barbatus*), fur seal (*Callorhinus alascanus*), ringed seal (*Phoca hispida*), husky dog (*Canis familiaris*), *Phoca* sp., and other undetermined seals in Alaska and the American Arctic and sub-Arctic regions.

Representative slides of the material, which Lyster (1940) identified as *C. semerme*, from the bearded seal (*Erignathus barbatus*) have been made available to the writer through the courtesy of Professor T. W. M. Cameron. Although the proboscis is introverted in most of these, the shape of the body and the dimorphic condition of the body spines in the two sexes provide the evidence for recognizing them as *C. validum*, a distinct species (Van Cleave, 1953).

ACCIDENTAL INFECTIONS.—In the tabulation of occurrence of *C. semerme* in North America, it seems probable that the infection in the husky dog was accidental. From specimens of the pelagic cormorant (*Phalacrocorax pelagicus pelagicus*) which were collected by Dr. E. L. Schiller on St. Lawrence Island, Alaska, a few specimens of *C. semerme* and one individual of *C. hadweni* were recognized in a mixed infection along with an undetermined species of *Corynosoma*. The last mentioned seems to be a normal parasite of the pelagic cormorant but *C. semerme* and *C. hadweni* appear to be accidental infections.

DOUBTED RECORD.—Cordero (1933) records *Arctocephalus australis* from Montevideo as definitive host but identification of the parasite is doubted.

The author cited no critical evidence supporting the specific identification beyond the statement that the material was identical with the descriptions and figures given by Forssell and Luehe. Since neither of these authorities gave details sufficient for positive differentiation of *C. semerme*, the present writer regards this account of the occurrence of *C. semerme* in the southern hemisphere as highly questionable.

RECORDS OF THE OCCURRENCE OF *C. semerme*.—

Host	Locality	Date	Collector	Accession number
<i>Phoca hispida</i>	Point Barrow, Al.	April, 1949	Rausch	VC 4269
<i>Phoca hispida</i>	Point Barrow, Al.	May 10, 1949	Rausch	VC 4310
<i>Phoca hispida</i>	Point Barrow, Al.	Oct. 1, 1949	Rausch	VC 4435
<i>Callorhinus alascanus</i>	Pribilof I.	?	Scheffer	VC 3991
"Spotted seal"	St. Lawrence I., Al.	Aug., 1950	Schiller	VC 4450
"Spotted seal"	St. Lawrence I., Al.	Aug., 1950	Schiller	VC 4458
"Seal" undet.	St. Lawrence I., Al.	Apr. 28, 1950	Rausch	VC 4430
"Seal" undet.	St. Lawrence I., Al.	Aug. 1, 1950	Schiller	VC 4447
"Husky dog"	Dundas, Devon I., Can.	?	Inst. Par.	VC 3046

***Corynosoma reductum* (von Linstow, 1905)**

(Text Figs. D and E; Plate 5, Figs. 48 to 50)

Synonym: *Echinorhynchus reductus* von Linstow, 1905.

In 1905, O. von Linstow presented a most unsatisfactory and incomplete diagnosis for a species, now recognized as a member of the genus *Corynosoma*, taken from *Phoca hispida* (= *P. foetida*) of West Taimyrland by the Russian Polar Expedition, 1900-03. Only small, immature individuals were recorded. Since that time there is no direct evidence that any subsequent worker has ever recognized this species on the basis of specimens encountered. In lists of species and in faunal lists the name is occasionally mentioned (Railliet and Henry, 1907; Porta, 1908; Meyer, 1931b, 1932; *et al.*) but nowhere in the literature is there any information supplementing the sketchy observation of von Linstow. In the extensive series of *Corynosomas* collected by Dr. Robert Rausch from seals of Alaska and the American Arctic, the writer encountered a few individuals from *Phoca hispida* of Point Barrow, Alaska, that were at first regarded as probably a new species on the basis of the distinctive body shape and spination and the inordinate size of the proboscis. In the last feature these individuals have a proboscis which is distinctly longer and wider than that which is recorded for any other member of the genus *Corynosoma* appearing in seals of the northern hemisphere. The body form of the largest of these is distinctively wedge-shaped with a very heavy and broad fore-trunk narrowing rapidly to a much smaller hind-trunk somewhat similar to that found in *C. strumosum* and like that figured in von Linstow's drawing of the hind-trunk of *C. reductum*. A detailed comparison of the scanty morphological data recorded for *C.*

reductum reveals fair agreement with the material from *P. hispida* of Alaska. Consequently, the new material serves as the basis for amplifying the description of *C. reductum* which was given for the first time in Van Cleave, 1953.

MATERIAL.—The original material of *C. reductum* has not been available for study. The extant descriptions are so incomplete that only a few highly distinctive features, such as the inordinately large proboscis, are available to make the species recognizable. Thirty-six individuals from North American hosts have served as the basis for formulating a re-description of *C. reductum*.

DIAGNOSIS.—In preserved specimens the largest individuals are about 10 mm long, with anterior end of fore-trunk greatly widened (2.5 to 3.6 mm) then reducing rather conspicuously to a progressively narrowing hind-trunk about (0.54 to 0.70 mm in diameter a short distance anterior to the genital opening). Fore-trunk carrying conspicuous spines which on the dorsal surface extend only to about the region of maximum diameter but ventrally extend well onto the hind-trunk, their total extent a little less than one-half the length of the entire trunk. On the fore-trunk the spines are so long and so thickly set that the tip of one spine often overlaps the base of the spine next beyond it. Many of the trunk spines sigmoidal, 0.064 to 0.110 mm in length and 0.011 to 0.016 mm in width. Genital spines large, broad, widely separated from the remainder of the trunk spines by a very wide unspined zone and the former are more numerous and larger in male (0.041 to 0.044 by 0.016 to 0.022 mm) than in the female, often entirely lacking in female or obscured by the copulatory cap.

Proboscis inordinately larger than in any other member of the genus found in the northern hemisphere, 1.0 to 1.6 mm in length by 0.40 to 0.58 mm in maximum diameter; in a typical female .04 mm wide at anterior extremity and increasing gradually to the level of the maximum diameter in the proximal fourth of the proboscis length. Armed with 24 to 26 longitudinal rows of 11 or 12 hooks each, of which only the basal 1 or 2 in each series lacks a prominent root. Roots of hooks at anterior extremity about same length as curved thorn but in hooks located more posteriorly on the proboscis the root is distinctly longer than the projecting thorn. Longest hooks from 0.090 to 0.140 mm long.

Neck fairly prominent, narrower than adjacent part of the fore-trunk, the latter reducing rapidly to fit the base of the narrow neck.

Ovoidal testes overlapping one another in the posterior region of the fore-trunk, extending anteriorly into the region of trunk spination but considerably removed from the posterior extremity of the proboscis receptacle. Six clavate or pyriform cement glands irregularly crowded immediately behind the testes.

Largest females crowded with developing embryos which are not fully mature, lacking the fully formed external membranes.

Intermediate hosts unknown.

Definitive host in northern Europe and North America: the ringed seal, *Phoca hispida*. Rare in occurrence.

The best specimens available for this study were taken October 1, 1949, by Dr. Robert Rausch at Point Barrow, Alaska (VC 4435), where they occurred along with a small number of *C. semerme* and *C. hadweni* in the intestine of the same specimen of *P. hispida*. The extensive series of seal parasites included in the present study included but one additional instance (VC 3500) of the occurrence of *C. reductum*. These were likewise taken from *P. hispida* but at an entirely different location. This material came from the mouth of the Clyde River of Baffin Island on January 4, 1940, in collections by the staff of the Institute of Parasitology, Macdonald College. While a rather extensive series is included in this last lot of material, only one individual has the proboscis extruded sufficiently to serve for specific identification. However, the extreme size of that one proboscis and the specifications of its hook armature supplement the observations available in other members of the series on body shape, size, distribution of trunk spines and the inordinately large genital spines. In the description of the species emphasis is placed upon the extreme size of the proboscis in *C. reductum*. This observation helps to explain the absence of proboscis on most of the specimens because with that organ deeply embedded in the host tissue the proboscis would become torn from the body in ordinary attempts at removal of the worms by pulling or by scraping the mucosa.

RECORDS OF THE OCCURRENCE OF *C. reductum*.—

Host	Locality	Date	Collector	Accession number
<i>Phoca hispida</i>	Clyde R., Baffin I.	Jan. 4, 1949	Inst. Par.	VC 3500
<i>Phoca hispida</i>	Point Barrow, Al.	Oct. 1, 1949	Rausch	VC 4435

***Corynosoma obtuscens* Lincicome, 1943**

(Text Figs. D and E; Plate 3, Figs. 34 to 49)

This species was described by Lincicome (1943) from specimens taken by C. M. Herman from the California sea lion at the San Diego Zoological Gardens. The description which follows is taken largely from the original publication to which information is added regarding second intermediate hosts. On superficial examination, a female of this species might be mistaken for *Corynosoma semerme*, since in much of the older literature it is assumed that continuous spination of the ventral surface of the trunk is specifically distinctive for that species. *C. obtuscens* provides a most interesting intermediate condition, in that trunk spines of the female continue uninterruptedly to the posterior extremity as in *C. semerme* while

in the male the trunk spination is interrupted, leaving an unspined zone of the hind-trunk anterior to the genital spines.

MATERIAL.—Three paratypes of *C. obtusens* in the collection of the writer have served as the direct basis for identification of five immature specimens of this species taken from cysts in the viscera of the leopard grouper (*Mycteroperca pardalis*). The fish intermediate host was obtained from commercial fishermen operating in the vicinity of Mazatlán, off the west coast of Mexico.

DIAGNOSIS.—Body small, its shape not conspicuously different in the two sexes. Females 2.2 to 3.0 mm long, males 2.0 to 2.8 mm. Fore-trunk swollen and usually bent ventrally, not sharply set off from the hind-trunk which tapers gradually toward the posterior extremity. Maximum dorso-ventral diameter of fore-trunk in females 0.7 to 1.0 mm, in males about 0.7 mm. Hind-trunk a short distance anterior to the genital extremity in females 0.4 to 0.7 mm in diameter, in males 0.3 to 0.5 mm. Fore-trunk with spines which dorsally extend posteriorly only to the region of maximum diameter but ventrally continue along the surface of the fore-trunk and in females continue uninterruptedly to the posterior extremity; in males the ventral spines of the hind-trunk are discontinued some distance immediately anterior to the genital spines. Fore-trunk spines 0.028 to 0.052 mm long by about 0.008 mm wide, the tip of each spine holding up a triangular elevation of the cuticula. Genital spines of male about 30 in number, acutely triangular, 0.029 to 0.048 mm long by 0.012 to 0.027 mm wide; in female no spines extending dorsal to the genital opening. In both sexes genital spines may be partially or wholly within introverted genital vestibule.

Neck short, often infolded around the base of the proboscis. Proboscis relatively small and narrow for a member of this genus, bent at a sharp angle with the axis of the body, slightly swollen near base. Proboscis 0.528 to 0.616 mm long in females, about 0.520 to 0.546 mm in males; width at anterior end 0.116 to 0.156 in females, 0.104 to 0.140 in males; at swollen region 0.180 to 0.204 in females, 0.144 to 0.180 in males; base a little wider than anterior region in both sexes. Proboscis hooks arranged in 16 to 19 longitudinal rows with 12 to 13 hooks in each row of which the basal 3 or 4 in each row are simple, thorn-like, with poorly developed roots. Anterior hooks in females ranging from 0.044 to 0.056 mm long, with a width at base of the thorn 0.008 to 0.018 mm; posterior to the swollen zone the hooks are 0.016 to 0.040 mm in length with a width of 0.004 to 0.012 mm. Hooks of males are somewhat smaller than those of females, on anterior region 0.036 to 0.056 mm long with a diameter of 0.008 to 0.016 mm; posterior to the swollen region 0.028 to 0.030 mm by 0.006 to 0.009 mm in diameter. Lemnisci short, flat.

Testes in anterior half of body, crowded diagonally side by side,

reaching forward beyond posterior tip of proboscis receptacle. Six pyriform cement glands clustered behind the testes. Genital opening subterminal, slightly dorsal in both sexes.

Embryos in body cavity of gravid females 0.068 to 0.092 mm in length by 0.020 to 0.028 mm wide, with a prolongation of the inner membranes at each pole.

First intermediate host unknown.

Second intermediate host. Ward and Winter (1952) reported the finding of immature individuals of *C. obtusens* in cysts of the mesenteries of the yellowfin croaker (*Umbrina roncadore*) taken in waters off Catalina Island in southern California. Also in the viscera of a leopard grouper (*Mycteroperca pardalis*) caught in the Gulf of California near Mazatlán, Mexico, three encysted juvenile worms, two females and one male, were taken by the present writer. Features of the proboscis and of trunk spination in the two sexes warrant identification of this material as juveniles of *Corynosoma obtusens*.

Definitive host: the California sea lion, *Zalophus californianus*, in captivity in the San Diego Zoological Gardens.

RECORDS OF THE OCCURRENCE OF *C. obtusens*.—

Host	Locality	Date	Collector	Accession number
<i>Zalophus californianus</i>	San Diego, Cal.	1941?	Herman	VC 3590
<i>Immature</i>				
<i>Mycteroperca pardalis</i>	Mazatlán, Mex.	May 10, 1940	Van Cleave	VC 3669
<i>Umbrina roncadore</i>	Catalina I., Cal.	July, 1949	Ward and Winter

***Corynosoma validum* Van Cleave, 1953**

(Text Figs. D and E; Plate 4)

Specimens taken in considerable numbers by Drs. Robert Rausch and E. L. Schiller from the Pacific walrus (*Odobenus divergens*) and from the bearded seal (*Erignathus barbatus*) have proboscides of very unusual shape and bodies of most distinctive form. The proboscis is almost perfectly cylindrical and is frequently nearly one-fifth the length of the entire worm. In body form there is a distinct sexual dimorphism. While the male (Fig. 41) has a short, tapering hind-trunk, not sharply set off from the fore-trunk and not so long as the fore-trunk, the body of the female (Fig. 40) is wholly devoid of any narrowed region at the posterior end. In the females the trunk is so highly inflated that the dorso-ventral diameter is often more than one-half the length of the entire trunk and a bluntly rounded point is all that might possibly be considered as the equivalent of the hind-trunk so characteristic of all other members of this genus.

MATERIAL.—A total of 192 permanent whole mounts of distinctive *C.*

validum form the basis for the following specific diagnosis. Of these, 89 have been designated as types.

DIAGNOSIS.—Body of female pouch-like, without attenuated posterior extremity, from 3.5 to 4.6 mm long, with maximum dorso-ventral diameter of 1.8 to 3.2 mm; males 3.9 to 5.4 mm long with maximum diameter of 1.8 to 2.7 mm, the posterior portion of trunk reducing rapidly to a diameter of 0.35 to 0.46 mm near the posterior extremity, especially in males with extroverted bursa. Neck short, diminishing rapidly from the diameter of the trunk to that of the base of the proboscis. Proboscis of both sexes cylindrical, that of female 0.8 to 1.0 mm long by 0.34 to 0.40 mm wide; of male 0.7 to 0.8 mm long by 0.27 to 0.35 mm wide. Proboscis armed with 22 or 24 longitudinal rows of 13 to 16 hooks each, of which the proximal 5 or 6 of each row are small, relatively crowded, and without recurved roots; anterior 9 or 10, with rooted hooks, not varying greatly in length but increasing gradually in diameter from the tip toward the base of the proboscis; none of the hooks conspicuously enlarged, in females commonly about 0.079 mm long by 0.026 mm thick where the thorn joins the root, in males about 0.064 to 0.069 mm long.

Trunk spines of female extending almost entire length of the body ventrally but only to the region of maximum diameter dorsally, often each spine is surrounded by a small, rounded cuticular papilla; in males the spines extend along the ventral surface to a point only a short distance posterior to the hind margin of the testes, much of hind-trunk devoid of spines except for the genital spines on the area immediately adjacent to the genital pore. Largest trunk spines usually 0.035 to 0.053 mm long in females, those of males usually a little shorter, 0.032 to 0.044 mm. Genital spines of males 0.035 to 0.053 mm long and 0.010 to 0.014 mm wide; ventral spines nearest female genital orifice 0.032 to 0.053 mm long, commonly not reaching the immediate vicinity of the aperture. Genital spines of males often completely withdrawn into the introverted genital vestibule.

Proboscis receptacle in male often reaching backward into the region of the cement glands; in female often extending through more than half the length of the trunk. Lemnisci broad, flat, lateral edges usually rolled. Shelled embryos in bodies of gravid females 0.090 to 0.116 mm long by 0.022 to 0.032 mm wide.

Intermediate hosts unknown.

Definitive hosts: the Pacific walrus (*Odobenus divergens*), the bearded seal (*Erignathus barbatus*), and unidentified seals in Alaska from St. Lawrence Island, Point Barrow, Kotzebue, and Wainwright. All available records restricted to North America. Holotype female (VC 4355.1) from the Pacific walrus (*Odobenus divergens*), Wainwright, Alaska, August, 1949, collected by Robert Rausch. Allotype male (VC 4429.6)

from same host species, St. Lawrence Island, Alaska, April, 1950, collected by Robert Rausch. Paratypes from same host species as holotype and allotype and also from bearded seal (*Erignathus barbatus*) VC 4309, taken by Robert Rausch at Point Barrow, Alaska.

Through the kindness of Professor Cameron, the specimens which Lyster (1940) identified as *C. semerme* from the bearded seal (*Erignathus barbatus*) have been examined and found to be *C. validum*.

COMPARISON.—*C. validum* is different from all other described species of *Corynosoma* in the shape of the body, which shows marked sexual dimorphism, the body of females having no cylindrical hind-trunk and being spined to a short distance anterior to the genital pore. The cylindrical proboscis, without basal enlargement, is likewise distinctive.

In collections of the British Museum of Natural History, the writer has seen a juvenile specimen from *Trematomus* or *Notothenia* collected by A. G. Bennett in the South Shetland Islands. This specimen had been apparently misidentified as *C. hamanni*. While it has a body form similar to that of *C. validum*, the proboscis is much smaller than in that species so that the two cannot be considered identical. No attempt has been made to name the specimen from the Antarctic.

RECORDS OF OCCURRENCE OF *C. validum*.—

Host	Locality	Date	Collector	Accession number
<i>Odobenus divergens</i>	Wainwright, Al.	Aug., 1949	Rausch	VC 4355
<i>Odobenus divergens</i>	St. Lawrence I., Al.	Apr. 28, 1950	Rausch	VC 4429
<i>Erignathus barbatus</i>	Point Barrow, Al.	May 15, 1949	Rausch	VC 4309
<i>Phoca</i> sp.	Kotzebue, Al.	May 2, 1949	Rausch	VC 4352
"Spotted seal"	St. Lawrence I., Al.	Aug., 1950	Schiller	VC 4458

***Corynosoma villosum* Van Cleave, 1953**

(Text Figs. D and E; Plate 5, Figs. 51 to 57)

Several collections of *Corynosoma*, primarily from Steller's sea lion (*Eumetopias jubata*) from various islands in the Bering Sea, are of uniform appearance and fail to agree in fundamental details with any other member of the genus. These are recognized (Van Cleave, 1953) as a distinct species under the name *Corynosoma villosum*.

MATERIAL.—*C. villosum* is one of the most abundantly represented species of the genus *Corynosoma* included in the present study. More than 200 stained permanent mounts have been studied in detail and from this long series 83 of the best specimens have been selected as critical material.

DIAGNOSIS.—Females 6.4 to 8.4 mm long by 1.78 to 1.85 mm in maximum diameter; males from 3.50 to 6.35 mm long by 1.36 to 1.60 mm in maximum diameter. Fore-trunk somewhat inflated but not sharply set off from the plump hind-trunk, the union of the two often recognizable

as a gradual merging rather than a sudden change in diameter. Anterior end of fore-trunk commonly in the form of a truncated cone, merging into the neck from which it is distinguishable by the fact that the narrowed fore-trunk bears spines. Hind-trunk of somewhat varying width, in females from 0.46 to 0.92 mm, in males from 0.42 to 0.69 mm. Neck short, about 0.173 mm long. Trunk spines restricted to anterior end of fore-trunk and extending its entire length ventrally but dorsally reaching only to about the level of the maximum diameter. Each spine tapering to a practically straight point; in females 0.029 to 0.041 mm long by 0.005 to 0.008 mm wide, in males they may reach 0.053 by 0.011 mm. Genital spines apparently lacking in some adult females, very prominent in some young females and in males; widely scattered over genital extremity, in some individuals tending toward sigmoidal form, in others flat and broadly triangular, 0.044 to 0.053 mm long by 0.012 to 0.019 mm wide.

Proboscis broadly vase-shaped, expanded in basal third, in females 0.69 to 0.76 mm long by 0.346 to 0.448 mm in maximum diameter, 0.208 to 0.230 mm wide in anterior region and approximately the same diameter at the base. Dimensions of proboscis of males only slightly smaller than in females. Distal tip of proboscis often tipped with a smoothly rounded hyaline cap (see Text Fig. E) extending about 0.058 mm beyond the most anterior hooks. Armature consists of 22 to 24 longitudinal rows of 12 or 13 hooks each, of which the basal 4 to 6 are simple, thorn-like, without recurved roots and closely set in the longitudinal rows. Anterior hooks not showing marked gradation in length but with gradual increase in width of the thorn from the tip posteriorly. None of the hooks inordinately enlarged, the root about the same length as the projecting thorn. Largest hooks of females 0.069 to 0.079 mm long and about 0.027 mm. in width at the bend where the thorn and root join; largest hooks of males 0.058 to 0.061 mm in length.

Edge of genital aperture of female (Fig. 55) slightly elevated as a lip-like ring, the swollen muscular vaginal sphincter filling the body cavity in the region of the pore where the body wall is very thin.

Testes of males ellipsoidal, extending into the posterior region of the fore-trunk, diagonally situated, reaching anteriorly to the level of the posterior end of the proboscis receptacle. Six clavate cement glands follow testes immediately, each about twice as long as broad.

Mature embryos within the body cavity of gravid females 0.098 to 0.140 mm long by 0.024 to 0.032 mm wide with a small rounded expansion of the membranes at each pole.

First and second intermediate hosts unknown.

Definitive hosts: type host Steller's sea lion (*Eumetopias jubata*) from various islands off the coast of Alaska. Also from the fur seal (*Callorhinus*

alascanus), Pribilof Islands, and from undetermined species of seals and the sea otter (*Enhydra lutris*) of Alaska.

Types: holotype male (VC 4443.1b) and allotype female (VC 4443.2a) from Steller's sea lion (*Eumetopias jubata*), St. Lawrence Island, Alaska, collected by E. L. Schiller, August, 1950. Paratypes from the same host species and same locality (VC 4443, VC 4444) as well as from East Cape, Amchitka, Aleutian Islands (VC 4570) collected by Robert Rausch, April 27, 1951; and from St. Paul Island of the Pribilof group collected by W. L. Jellison (VC 4583), September 8, 1951.

COMPARISONS.—*C. villosum* differs from all other species of the genus *Corynosoma* in general shape and size of the body and in shape, size, and armature of the proboscis. The proboscis in shape comes nearest to that of *C. reductum* but that of *villosum* is much smaller although it carries more and smaller hooks in each longitudinal row than does that of *C. reductum*. The genital spines are much larger than those found on *C. strumosum*.

RECORDS OF THE OCCURRENCE OF *C. villosum*.—

Host	Locality	Date	Collector	Accession number
<i>Eumetopias jubata</i>	St. Lawrence I., Al.	Aug., 1950	Schiller	VC 4443
<i>Eumetopias jubata</i>	St. Lawrence I., Al.	Aug., 1950	Schiller	VC 4444
<i>Eumetopias jubata</i>	Aleutian I.	Apr. 17, 1951	Rausch	VC 4570
<i>Eumetopias jubata</i>	St. Paul I., Al.	Sept. 8, 1951	Jellison	VC 4583
<i>Eumetopias jubata</i>	St. Paul I., Al.	June 2, 1947	Scheffer	VC 4054
<i>Callorhinus alascanus</i>	Pribilof I.	?	Scheffer	VC 3991
<i>Enhydra lutris</i>	Amchitka I., Al.	?	Rausch	VC 4516
<i>Enhydra lutris</i>	Amchitka I., Al.	?	Rausch	VC 4357
<i>Enhydra lutris</i>	Amchitka I., Al.	Mar. 14, 1952	Rausch	VC 4623
"Seal," undet.	St. Lawrence I., Al.	Aug., 1950	Schiller	VC 4447

***Corynosoma cameroni* Van Cleave, 1953**

(Text Figs. D and E; Plate 3, Figs. 30 to 33)

Professor T. W. M. Cameron submitted to the writer a series of collections of *Corynosoma* brought together by the staff of the Institute of Parasitology of Macdonald College from several autopsies of the white whale, *Delphinapterus leucas*. According to a preliminary report by Lyster (1940), only those white whales from the Gulf of St. Lawrence were infected by *Acanthocephala* while a single individual from Baffin Island, another from Ellesmere Island, and yet another from Southampton Island were free from *Corynosoma*. A single example of the white whale from Alaska, examined by Dr. Rausch, contained a single undetermined specimen of *Corynosoma* which is not identical with the material from the Gulf of St. Lawrence.

Lyster (1940:403) identified the specimens from the white whale of the Gulf of St. Lawrence as *Corynosoma strumosum*. The materials which the present writer has examined from the same collections do not con-

form to the concept of *C. strumosum* in shape or proportions of the body or in shape and armature of the proboscis. In a long series of very poorly preserved individuals there are but a few which show the proboscis clearly and these agree with the specimens with introverted proboscis in distinctive features of the body size, shape, and proportions. A distinct species (Van Cleave, 1953) is recognized for the material from the white whale of the Gulf of St. Lawrence under the name of *C. cameroni*.

MATERIAL.—*C. cameroni* is based upon a study of 39 stained permanent mounts all of which have been included in the type series.

DIAGNOSIS.—Body in both sexes short and plump, from 2.5 to 3.6 mm long by 0.9 to 1.6 mm in maximum dorso-ventral diameter. Hind-trunk often no longer than fore-trunk, the former with bluntly truncated termination and approximately about one-half the diameter of the fore-trunk. With no conspicuous constriction dividing the fore- from the hind-trunk. Trunk spination not extending posteriorly much beyond the fore-trunk on the ventral surface and reaching only a short distance along the dorsal surface. Trunk spines small, sigmoidal, about 0.026 to 0.035 mm long with a diameter of 0.008 to 0.014 mm, occasionally with a basal portion directed anteriorly at right angle to the projecting point but more often the proximal region is wide, narrowing without conspicuous bending except for a definite bend posteriorly near the tip. Genital spines lacking in immature females hence their absence is not due to removal with the shedding of the copulatory cap; in males comprising a large number of closely set spines, often introverted into the genital vestibule; commonly 0.026 mm long by 0.008 mm wide.

Neck short, in all available specimens inturned around the base of the proboscis in the anterior end of the fore-trunk. Proboscis subcylindrical without conspicuous enlargement in basal region; 0.7 to 0.9 mm in length with maximum width of 0.32 to 0.41 mm; armed with 16 longitudinal rows of 9 to 11 hooks each of which the proximal 4 or 5 of each row are smaller than those anterior to them and are commonly crescentic in shape. Largest hooks 0.105 to 0.132 mm long with a width of 0.038 to 0.046 mm at the bend where the thorn and root meet; anterior hooks usually 0.055 to 0.095 mm long by 0.022 mm wide. Proboscis receptacle often reaching posteriorly into the hind-trunk.

No individuals of either sex fully mature.

Intermediate hosts unknown.

Definitive host: *Delphinapterus leucas*, the white whale, in the Lower Gulf of St. Lawrence, Province of Quebec, Canada.

Types: holotype female (VC 3502.3) from white whale (*Delphinapterus leucas*) White Banks, Gulf of St. Lawrence, Quebec, August 7, 1938. Allotype male (VC 3505.4) from same host species and same lo-

cality, taken September 24, 1938. Holotype, allotype, and a series of paratypes, representing both sexes, from the same host species and same general locality. The following paratypes are deposited in the Institute of Parasitology, McGill University, Macdonald College, Quebec; VC 3502.5, VC 3504.6, VC 3504.10, VC 3505.1, VC 3505.2, VC 3505.5, VC 3505.6.

COMPARISONS.—*C. cameroni* differs from all other species of the genus from mammals in the northern hemisphere in the shape of the short, thickset body with hind-trunk often no longer than the fore-trunk and commonly about one-half the diameter of the fore-trunk. The proboscis is larger than that of all other species from mammals of the Holarctic except *C. validum*, *C. reductum*, and *C. hadweni*; in shape as well as in number and differentiation of the hooks it is distinctly different from each of these. The proboscis is wider than that of *C. hadweni* and lacks the basal swelling; it is shorter and has fewer hooks than in *C. reductum*; and there is a much smaller number of hooks with greater differentiation of the hooks when compared with *C. validum*.

RECORDS OF THE OCCURRENCE OF *C. cameroni*.—

Host	Locality	Date	Collector	Accession number
<i>Delphinapterus leucas</i>	White Banks, Que.	Aug. 1, 1938	Inst. Par.	VC 3501
<i>Delphinapterus leucas</i>	White Banks, Que.	Aug. 7, 1938	Inst. Par.	VC 3502
<i>Delphinapterus leucas</i>	White Banks, Que.	Aug. 3, 1938	Inst. Par.	VC 3503
<i>Delphinapterus leucas</i>	White Banks, Que.	Sept. 23, 1938	Inst. Par.	VC 3504
<i>Delphinapterus leucas</i>	White Banks, Que.	Sept. 24, 1938	Inst. Par.	VC 3505

***Corynosoma hadweni* Van Cleave, 1953**

(Text Figs. D and E; Plates 6 and 7)

The first large number of specimens of the genus *Corynosoma* from seals which the writer had the opportunity to study were taken by the late Dr. Seymour Hadwen, at Unalaska Island of the Aleutian chain in Alaska, December 4, 1920, and January 21, 1921. The hosts were grey seals (*Halichoerus grypus*) and memoranda taken at the time of collecting indicated that some were taken from the small intestine and others were removed from fecal material of the hosts but the two groups were not kept separate. Nearly thirty years ago the writer began the study of this material and difficulties which were then apparent remained unsolved until recently. Information regarding the American representatives of the genus *Corynosoma* was wholly unavailable and it seemed to be a common assumption that the marine mammals of the Arctic realm probably carried the same species of *Acanthocephala* throughout their range. Only the seals of northern Europe had been examined carefully

and but two species of *Corynosoma* had been commonly recognized in them. A preliminary study revealed the fact that no specimen from the Alaskan collection had the continuous trunk spination similar to that distinctive for *Corynosoma semerme*. Since the pattern of spination was similar to that found in *C. strumosum*, the specimens were tentatively assumed to represent that species. However, further observation demonstrated the fact that if a single species were here involved, the individuals of that species must have a range of individual variability far in excess of anything that had been previously recorded for a number of the genus *Corynosoma*. Finally tabulation of the assembled data demonstrated the fact that the specimens fall readily into three distinct groups with very little intergrading of any of the morphological features.

As the writer became more familiar with conditions encountered in a study of several long series of representatives of *Corynosoma*, it became increasingly clear that one of these groups was identifiable as *C. strumosum*. From this group the other two are readily separable on morphological features involving particularly the proboscis, its shape and armature. These differences are so obvious that the two other groups have been regarded as separate species. The names *C. hadweni* and *C. falcatum* are applied to these species (Van Cleave, 1953) which are described and differentiated in the following paragraphs.

MATERIAL.—More than 150 permanent mounts of stained specimens of *C. hadweni* have been examined critically in the present study. Of this series 106 of the best specimens have been designated as critical type material.

DIAGNOSIS.—Body moderately robustly elongated, without difference between members of the two sexes. Enlarged fore-trunk about three-eighths the length of the entire trunk, its front end fairly evenly rounded, ovoidal in shape with the largest diameter anteriorly, the dorsal surface somewhat more inflated than the ventral; posteriorly tapering to meet the diameter of the nearly cylindrical hind-trunk which is only about one-fifth to two-fifths the width of the fore-trunk. Total length 6.00 to 8.25 mm with maximum dorso-ventral diameter of 1.43 mm in males and 1.43 to 2.50 mm in females. Trunk spines not conspicuous, along ventral surface usually not extending posteriorly much beyond the swollen fore-trunk and dorsally reaching only a short distance from the anterior extremity of the trunk; largest 0.026 to 0.046 mm long by 0.008 to 0.014 mm wide. Genital spines entirely separate from trunk spines 0.024 to 0.035 mm long by about 0.010 mm wide, somewhat sigmoidal in form, often entirely obscured.

Neck fairly long, narrow, a truncated cone approximately as long as

the proboscis. Proboscis with a fairly conspicuous enlargement of the basal third carrying hooks much larger and heavier than on rest of proboscis. Proboscis length 0.84 to 0.93 mm, with a maximum diameter of 0.30 to 0.37 mm, commonly about 0.23 mm in narrowed anterior third. Armed with 16 longitudinal rows of 10 or 11 hooks each, of which the proximal 5 or 6 are simple, thorn-like, fairly closely crowded in the row and as a series rather widely separated from the greatly enlarged hooks anterior to them. Anterior hooks progressively increasing in diameter from the anterior tip of proboscis, with conspicuous root of each usually about the same length as the projecting thorn. Hooks near distal tip 0.079 to 0.104 mm long with a dorso-ventral width of 0.004 to 0.016 mm at the bend where the thorn joins the root; largest hooks 0.105 to 0.150 mm long with width of 0.026 to 0.041 mm; basal hooks with the distal one-third or one-half bent posteriorly, almost at right angle to the basal part; straight line measurement from tip to root 0.046 to 0.061 mm with diameter of 0.005 to 0.011 mm.

Testes about twice as long as wide, the anterior one reaching into the cavity of the fore-trunk. Cement glands very long, tubular.

Embryos within bodies of mature females 0.093 to 0.115 mm long by 0.020 to 0.035 mm wide, with rounded internal prolongation at each pole.

First intermediate host unknown.

Second intermediate host: cystacanths removed from visceral cysts of the smelt, *Osmerus mordax*, collected by Dr. Marvin C. Meyer, Maine.

Definitive hosts: the grey seal (*Halichoerus grypus*), Unalaska Island, Aleutian Chain, Alaska, taken in December and January by the late Dr. Seymour Hadwen; ringed seal (*Phoca hispida*), Point Barrow, Alaska, taken in April and May by Dr. Robert Rausch; unidentified seals of the genus *Phoca*, St. Lawrence Island, Alaska, in April and May and at Kotzebue, Alaska, in May by Dr. Robert Rausch.

A single immature individual of *C. hadweni* was included in a mixed infection of *Corynosoma* taken from a pelagic cormorant (*Phalacrocorax pelagicus pelagicus*) of St. Lawrence Island, Alaska, by Dr. E. K. Schiller. This must be regarded as an accidental infection.

Types: holotype female (VC 4311.1) from ringed seal (*Phoca hispida*) taken at Point Barrow, Alaska, by Robert Rausch, May 5, 1949; allotype male (VC 4432.1) from undetermined seal taken in Alaska by Robert Rausch, May 1, 1950. Paratypes of both sexes from various other seals in Alaska and from the mouth of the Clyde River, Baffin Island.

COMPARISONS.—*C. hadweni* most closely resembles *C. strumosum* and *C. reductum*. It differs from both of these in many respects of which the most readily observable are the size, shape, and proportions of the body, the size of the proboscis, and the number and sizes of the individual hooks.

RECORDS OF THE OCCURRENCE OF *C. hadweni*.—

Host	Locality	Date	Collector	Accession number
<i>Halichoerus grypus</i>	Unalaska, Al.	Dec. 4, 1920	Hadwen	VC 1932
<i>Halichoerus grypus</i>	Unalaska, Al.	Dec. 4, 1920	Hadwen	VC 2637
<i>Halichoerus grypus</i>	Unalaska, Al.	Jan. 21, 1921	Hadwen	VC 1933
<i>Phoca hispida</i>	Clyde R., Baffin I.	Jan. 4, 1940	Inst. Par.	VC 3497
<i>Phoca hispida</i>	Point Barrow, Al.	Apr., 1949	Rausch	VC 4268
<i>Phoca hispida</i>	Point Barrow, Al.	Apr., 1949	Rausch	VC 4269
<i>Phoca hispida</i>	Kotzebue, Al.	Apr. 19, 1949	Rausch	VC 4353
<i>Phoca hispida</i>	Point Barrow, Al.	May 5, 1949	Rausch	VC 4311
<i>Phoca hispida</i>	Point Barrow, Al.	May 13, 1949	Rausch	VC 4310
<i>Phoca hispida</i>	Point Barrow, Al.	Oct. 1, 1949	Rausch	VC 4435
<i>Erignathus barbatus</i>	Point Barrow, Al.	May 15, 1949	Rausch	VC 4309
<i>Phoca</i> sp.	Kotzebue, Al.	May 2, 1949	Rausch	VC 4352
<i>Phoca</i> sp.	Unalakeet, Al.	May 5, 1949	Rausch	VC 4354
Spotted seal	St. Lawrence I., Al.	Aug., 1950	Schiller	VC 4450
Seal, undet.	St. Lawrence I., Al.	Apr. 28, 1950	Rausch	VC 4428
Seal, undet.	St. Lawrence I., Al.	Apr. 28, 1950	Rausch	VC 4430
Seal, undet.	St. Lawrence I., Al.	May 1, 1950	Rausch	VC 4431
Seal, undet.	St. Lawrence I., Al.	May 1, 1950	Rausch	VC 4432
<i>Immature</i>				
<i>Osmerus mordax</i>	Maine	July 21, 1948	Meyer	VC 4152
<i>Osmerus mordax</i>	Maine	Apr. 2, 1949	Meyer	VC 4216

***Corynosoma falcatum* Van Cleave, 1953**

(Text Fig. E; Plate 1, Fig. 16)

Some specimens mixed with *C. strumosum* and *C. hadweni* from the grey seal (*Halichoerus grypus*) show marked peculiarities in the shape and size of the proboscis and the form of the proboscis hooks. The first one of these under observation was regarded as a teratological specimen, but when several having the same appearance were discovered it became evident that a distinct species would need to be recognized and to this concept the name *C. falcatum* has been applied (Van Cleave, 1953).

MATERIAL.—A total of eight specimens of *C. falcatum* has been examined in the present study. These constitute the type material.

DIAGNOSIS.—Body moderately robust, with inflated fore-trunk and practically cylindrical hind-trunk, the latter bluntly rounded at its posterior extremity. Body shape not conspicuously different in the two sexes but females larger than males. Total length of females 6.00 to 7.27 mm, maximum width of fore-trunk 1.25 to 1.97 mm; males 4.6 to 5.3 mm in length by 1.07 to 1.25 mm in maximum width; in largest females the hind-trunk is 0.40 to 0.57 mm in diameter, in males about 0.23 to 0.40 mm. Trunk spination never conspicuously developed, faintly discernible on front end of fore-trunk but no spines on the hind-trunk. Genital spines not observed in either sex. Neck short. Proboscis frequently cylindrical with but a slight swelling just posterior to the middle, 0.690 to 0.865 mm long by 0.208 to 0.300 mm in maximum diameter; armed with 14 longitudinal

rows of 10 or 11 hooks each, of which the basal 4 or 5 (6 in some specimens) are small and of very irregular shape, often lacking sharp point, not crowded in the row. Largest hooks 0.075 to 0.115 mm in length, distinctly falciform or sickle-shape, in some instances as much as 0.026 to 0.041 mm in width at the bend where thorn joins root; at times the tip forming a nearly closed loop or short tip region bent at almost right angle to the enlarged basal part of the thorn. Hooks sparsely distributed over the proboscis, many lacking distinct root and often deformed in shape. Largest hooks, at level of maximum diameter of proboscis or anterior to it on the anterior slope leading to the enlargement.

Male reproductive organs confined to the cylindrical portion of the hind-trunk. Testes slightly longer than broad, considerably overlapping one another, not reaching to the level of the proboscis receptacle. Cement glands short, pyriform, crowded immediately behind testes. Embryos in body of fully gravid females 0.069 to 0.093 mm long and 0.019 to 0.024 mm wide, with a small, rounded expansion of inner membranes at each pole.

Intermediate hosts unknown.

Definitive host: the grey seal (*Halichoerus grypus*), Unalaska, Alaska, collected in December and January.

Types: holotype female (VC 2637.16), allotype male (VC 2637.17) and six paratypes, all from grey seal (*Halichoerus grypus*) taken at Unalaska, Alaska, December 4, 1920, by Seymour Hadwen.

COMPARISON.—*C. falcatum* differs from all other species of the genus in the number and peculiar shape of the proboscis hooks and in deformity of the basal hooks in each row. It differs from *C. strumosum* and *C. hadweni*, from the same host species, in that the length of the proboscis of *C. falcatum* is about intermediate in length between them, with but rarely any individuals intergrading in length. There are also fewer longitudinal rows of proboscis hooks in *C. falcatum* than in the other two.

RECORD OF THE OCCURRENCE OF *C. falcatum*.—

Host	Locality	Date	Collector	Accession number
<i>Halichoerus grypus</i>	Unalaska, Al.	Dec. 4, 1920	Hadwen	VC 2637

Unidentifiable Corynosomas.—The present writer is in full agreement with the thoughts of H. W. Stunkard (1948) when he expressed concern over the impossibility of associating names of previously described species of tapeworms from pinnipeds with specimens encountered in collections. It is extremely unfortunate under circumstances of this sort when the confusion of descriptions is so great that numbers rather than names are used to specify the various recognizable concepts. This offers no solution for the problem and regardless of how carefully the diagnoses of the numbered concepts may be drawn the responsibility for decision

on problems of validity and synonymy are merely postponed and a new series of concepts is added to make the confusion more severe.

As mentioned previously in this survey, the descriptions of previously named species of *Corynosoma* are far from perfect or complete but all the names proposed for species from the northern hemisphere are now recognizable as either valid species or synonyms. Down to the present date three species of *Corynosoma* have been generally recognized in the marine mammals of North America. These include the two well-known European species *C. strumosum* and *C. semerme* together with *C. obtusens* which seems to be restricted to this continent. In the course of the present study a fourth inadequately known species, *C. reductum*, previously known from Eurasia only has been rediscovered in the New World. This study, which has extended over about thirty years, has brought to light five additional species from North American mammals, *C. hadweni*, *C. falcatum*, *C. villosum*, *C. validum*, and *C. cameroni*, bringing to nine the number of species of *Corynosoma* from North American mammals. As a summary of an extended program of research, this sounds like a relatively simple, straight-forward announcement of results but not all of the problems of specific identification have been solved.

After the foregoing species of *Corynosoma* had been recognized, there remained an irresolvable residue of unnamed materials in the collection of the writer. Much of this is doubtless material of the other species which fails to show distinctive specific characters, probably because of poor preservation. In several lots of specimens no proboscis is observable, either because it is always completely introverted, due to improper treatment before preservation, or because the worms were forcibly pulled from the host intestine, severing the body of the worms from their proboscides which were left buried in host tissues. It has been emphasized throughout this section that most species of *Corynosoma* lack rigid host specificity, consequently there is no security in assigning the defective material to species previously recorded for the same host.

In one instance a single individual (Fig. 29) from the sea otter (*Enhydra lutris*) of Simeonof Island, collected by V. B. Scheffer, is wholly unlike any of the species taken from that host or from any other mammal. Although more than half of the proboscis is introverted, that organ is entirely different from that known for any other species of *Corynosoma*, including the *C. enhydris* described from this host by Afanas'ev (1941) in his work on the otters of the Commander Islands. Too many of the important morphological details are lacking to warrant description of this individual as type of a new species.

In the following list of unidentified specimens, it is probable that most of the specimens are unrecognizable representatives of previously recognized species.

RECORDS OF THE OCCURRENCE OF UNIDENTIFIED SPECIES OF CORYNOSOMA.—

Host	Locality	Date	Collector	Accession number
<i>Phoca hispida</i>	Payne Bay, N.W.T.	Jan. 4, 1940	Inst. Par.	VC 3496
<i>Phoca hispida</i>	Clyde R., Baffin I.	Jan. 4, 1940	Inst. Par.	VC 3497
<i>Phoca hispida</i>	Point Barrow, Al.	Apr. 19, 1949	Rausch	VC 4353
<i>Phoca hispida</i>	Point Barrow, Al.	May 13, 1949	Rausch	VC 4310
<i>Phoca hispida</i>	Point Barrow, Al.	May 5, 1949	Rausch	VC 4311
<i>Phoca hispida</i>	Point Barrow, Al.	Oct. 1, 1950	Rausch	VC 4435
<i>Phoca vitulina</i>	Lake Harbor, Baffin I.	Jan. 4, 1949	Inst. Par.	VC 3499
<i>Enhydra lutris</i>	Simeonof I., Al.	June 2, 1947	Scheffer	VC 4054
<i>Eumetopias jubata</i>	St. Paul I., Al.	July 12, 1948	Scheffer	VC 4169
"Spotted seal"	St. Lawrence I., Al.	Aug., 1950	Schiller	VC 4458
"Seal"	St. Lawrence I., Al.	May 1, 1950	Rausch	VC 4432
"Seal"	St. Lawrence I., Al.	Apr. 27, 1950	Rausch	VC 4427
"Seal"	St. Lawrence I., Al.	May 28, 1950	Rausch	VC 4430
"Seal"	Havre St. Pierre, Que.	Jan. 4, 1940	Inst. Par.	VC 3498

Diversity of Faunas.—Only three generally recognized valid species of *Corynosoma* are recorded from mammals of northern Europe and Asia. The status of *C. enhydris*, a possible fourth species, is still somewhat in doubt. Several additional species that have been proposed have been reduced to synonymy. These same three species (*C. strumosum*, *C. semerme*, and *C. reductum*) are all found in mammals of North America and in addition there are six other species which seem to be restricted to this continent. One of these (*C. obtusens*) had been described previously and five more species have been added in the course of the present study (*C. validum*, *C. villosum*, *C. hadweni*, *C. falcatum*, *C. cameroni*). Comparisons have been made and checks have been imposed to ensure that the differences between the faunas of the two hemispheres are not merely subjective, due to the application of diverse concepts of species.

No satisfactory hypothesis is available to explain fully the different rates of speciation in *Corynosomas* of marine mammals of the two hemispheres. However, it is interesting to note that in another group of Acanthocephala, the family Neoechinorhynchidae, there has been extensive differentiation of species and even of genera in North America, while that family has remained practically static in northern Europe. It has been pointed out that in America the differentiation of a distinctive fish fauna has been paralleled by the diversification of the Neoechinorhynchidae (Van Cleave, 1949a; Van Cleave and Bangham, 1950) which have undergone marked evolutionary change at both specific and generic levels along with the evolution of the distinctive fish fauna of North America. There has been no comparable degree of speciation in the Neoechinorhynchidae of European fishes. The comparisons between the continental distribution and speciation in Neoechinorhynchus and *Corynosoma* extends still further. While each of these genera has at least one species which is widely distributed in both hemispheres (Van Cleave

and Lynch, 1950; Van Cleave, 1953), there are additional species in each genus which are peculiar to the North American fauna. That this observation is not attributable to the application of different standards for species concepts is borne out by the fact that the present writer has examined representative collections of both genera concerned from European hosts and has found no evidence of diversification of species in the European fauna comparable to that which is so conspicuous in the American fauna.

The extrinsic factors operating to produce evolutionary change in Acanthocephala must be sought primarily in the conditions provided by the bodies of the two or more essential hosts, because in members of this phylum the individual is never exposed directly to the effects of the physical environment (Van Cleave, 1953). Especially in the definitive host, relatively small, isolated populations are forced to interbreed and thereby any new character that arises has the opportunity to become established. Although the factors have not been analyzed, it seems evident that in the genus *Corynosoma*, as well as in the family Neoechino-rhynchidae, conditions conducive to evolutionary change have been more favorable in hosts of the western hemisphere than in hosts of the continents to the east.

Key to the Species of the Genus Corynosoma Occurring as Adults in Mammals of North America.—

1. (a) Proboscis essentially cylindrical, without conspicuous enlargement near base and lacking greatly enlarged specialized hooks. Body of female lacking cylindrical hind-trunk of reduced diameter.—*C. validum* Van Cleave, 1953.
- (b) Proboscis with somewhat of an enlargement near its base, bearing hooks heavier than those located more anteriorly.—2.
2. (a) Trunk spines extending almost entire length of the ventral surface of female.—3.
- (b) Trunk spines never extending along ventral surface the full length of the hind-trunk.—4.
3. (a) Proboscis hooks in 20 to 22 longitudinal rows. Trunk spines extending the full length of the trunk along the ventral surface in both sexes.—*C. semerme* (Forssell, 1904).
- (b) Proboscis hooks in 16 to 19 longitudinal rows. Trunk spines of male ending considerable distance anterior to the region bearing genital spines.—*C. obtusens* Lincicome, 1943.
4. (a) Proboscis with more than 20 longitudinal rows of hooks.—5.
- (b) Proboscis with less than 20 longitudinal rows of hooks.—6.
5. (a) Proboscis over 1 mm long, its largest hooks 0.090 to 0.140 mm long; small hooks at distal end of each row limited to one or two.—*C. reductum* (von Linstow, 1905).

- (b) Proboscis under 0.8 mm long, its largest hooks 0.060 to 0.079 mm long; four or five small hooks at distal end of each longitudinal row.—*C. villosum* Van Cleave, 1953.
- 6. (a) Cylindrical hind-trunk shorter than fore-trunk.—*C. cameroni* Van Cleave, 1953.
- (b) Cylindrical hind-trunk considerably longer than the fore-trunk.—7.
- 7. (a) Proboscis under 0.6 mm in length. Genital spines numerous, ordinarily covering a considerable area at the posterior end of the trunk.—*C. strumosum* (Rudolphi, 1802).
- (b) Proboscis usually more than 0.65 mm long. Genital spines inconspicuous or lacking.—8.
- 8. (a) Genital spines lacking. Large proboscis hooks all sickle-shaped, many of the hooks deformed.—*C. falcatum* Van Cleave, 1953.
- (b) Genital spines present but inconspicuous, not widely distributed. Proboscis hooks regular in shape, the thorn being sharply pointed and straight.—*C. hadweni* Van Cleave, 1953.

XII. PRELIMINARY ANALYSIS OF THE GENUS BOLBOSOMA IN NORTH AMERICA

GENUS BOLBOSOMA Porta, 1908

Synonyms: *Bolborhynchus* Porta, 1906.

Echinorhynchus Zoega, in Mueller, 1776, in part.

Pomphorhynchus of Leiper and Atkinson, 1915.

Diagnosis of Bolbosoma.—With the characters of the subfamily Polymorphinae. Body of moderate size (10 mm) to large (over 200 mm) in length. Never with trunk spines in region of the genital extremity. Anterior extremity of trunk modified as an inflated bulb or slightly expanded in diameter, characteristically provided with a covering of relatively large trunk spines which do not extend beyond the inflated region and are usually arranged as two separate collars or spine fields.

The region immediately posterior to the trunk bulb is reduced in diameter by a constriction which may be either short or relatively long and sharply demarcated from the hind-trunk or articulated with it through gradual transition in body diameter. Neck short, cylindrical or in the form of a truncated cone, unspined. Proboscis conical, cylindrical, or club-shaped, its strong hooks with prominently recurved simple roots except for a few simple thorns at the base of each longitudinal row of hooks. Proboscis receptacle a double-walled, closed, muscular sac. Lemnisci simple, narrowly cylindrical, of variable length. Testes rounded or ellipsoidal, in contact with each other or slightly separated. Cement glands elongate, tubular. Fully formed embryos in body cavity of gravid female relatively large, with a relatively long polar prolongation of the middle membranes at each pole.

Definitive hosts: marine mammals, chiefly whales, of all oceans. First intermediate host probably crustaceans; second intermediate host: various marine fishes.

Although earlier investigators often recorded the occurrence of *Acanthocephala* in whales, Shipley (1899b, 1900) and Porta (1906, 1909) were among the earliest to treat of *Acanthocephala* of cetaceans as a group.

The writer can find no evidence that a type species has even been designated for the genus *Bolbosoma*. Stiles and Hassall (1920) indicate that since *Bolbosoma* is but a renaming of *Bolborhynchus* it should carry the same type as designated for the earlier name. However, no

type species has been named and in consequence *Bolbosoma balanae* (Gmelin, 1790) is here designated as type of the genus.

History of Bolbosoma.—Antonio Porta (1906) recognized the species of large Acanthocephala from whales as comprising a distinctive generic unit under the preoccupied name *Bolborhynchus*. In 1908, Porta proposed a new name, *Bolbosoma*, to replace the invalid *Bolborhynchus*. Since that date the genus has been very widely recognized and accepted although Leiper and Atkinson (1915) made a misguided effort to substitute the name *Pomphorhynchus* for it under the erroneous spelling “*Pomporhynchus*.” In so doing it is probable that they took the original indefinite diagnosis for *Pomphorhynchus* which Monticelli proposed in 1905 when only the presence of a bulla was cited in the characterization. However, they attributed the use of the name to Porta, which was an obvious error. In fact, Porta (1906:269) clearly differentiated between the two morphologically distinct types of bulla, indicating that a swelling of the neck is characteristic of *E. proteus*, representing the genus *Pomphorhynchus*, while an inflation of the trunk is responsible for the bulla in the Acanthocephala from cetaceans to which he applied the generic name *Bolborhynchus* (= *Bolbosoma*).

In his 1906 publication, Porta assigned five species to *Bolborhynchus*: *E. porrigens* Rudolphi, *E. capitatus* von Linstow, *E. pellucidus* Leuckart, *E. brevicolle* Malm, and *E. turbinella* Diesing. An indication of the relative stability of the concepts but not the names of cetacean Acanthocephala is found in the fact that Meyer (1932) recognized the same five concepts, although for two of them he accepted what he regarded as prior names: *B. vasculosum* (Rudolphi, 1819) (instead of *B. pellucidum* of Leuckart), and *B. balanae* (Gmelin, 1790) (to replace *B. porrigens* of Rudolphi). In addition to the initial list of species, Meyer recognized four names of later origin; *B. hamiltoni* Baylis, 1929 (from the Antarctic), *B. caenoforme* (Heitz, 1920), *B. heteracanthae* (Heitz, 1920), and ?*B. serpenticola* (Fukui, 1929). The last of these Meyer placed in the genus *Bolbosoma* with reservation. Since all of the last three are based upon immature individuals from intermediate hosts they do not add materially to an understanding of the genus.

American Material.—Knowledge regarding the genus *Bolbosoma* in North America has always been extremely meager. Leidy (1890:413) identified as “*E. pelludicus* Leuckart” specimens which Dr. Cooper Curtice had collected from a beaked whale “*Mesoplodon sowerbiensis*” (= *M. bidens*). In 1894, Stiles and Hassall recorded this same material as *E. pellucidus* in their listing of animal parasites from the various American collections to which they had access. When the present writer (Van Cleave, 1925) examined the Leidy collections, this material was not included since it had apparently remained in the collections of the

Smithsonian Institution. Specimens from the latter collection were later examined and the identification as *E. pellucidus* was supported, but following the nomenclature adopted by Monticelli (1905) the name *B. aurantiacum* was used in the published report (Van Cleave, 1925). More recently Meyer (1932) has regarded both *B. pellucidum* and *B. aurantiacum* as direct synonyms of *B. vasculosum* (Rudolphi, 1819). In accepting this synonymy, *B. vasculosum* is the only representative of the genus previously reported from whales of North America.

Linton (1891:534) recorded the presence of larval worms in the peritoneum of a sea bass, *Centropistes striatus* (= *Serranus atrarius*) from the Atlantic coast in the region of Woods Hole, Massachusetts. To this material he applied the name "*Echinorhynchus serrani*" under the assumption that it represented a separate species. The illustration shows that Linton was dealing with an immature specimen of the genus *Bolbosoma* but the status of the species has never been determined with certainty. Sumner, Osborn, and Cole (1913:756), in recording the parasites of *Centropistes striatus* in the fauna of the Woods Hole region, entered "*E. aurantiacum*" as presumably a correction for the earlier record of *E. serrani* given by Linton. Porta (1907) had suggested this synonymy.

Through personally negotiating the exchange of collections and loans of acanthocephalan materials, the writer has accumulated a representative collection of the genus *Bolbosoma* for study and for comparative purposes. These have come from many parts of the earth, from various countries of Europe, Africa, Japan, and New Zealand. In these collections are included representatives of most of the well-established species (*B. capitatum*, *B. vasculosum*, *B. balanae*, *B. turbinella*, and *B. brevicolle*) although some of the species based upon immature individuals from intermediate hosts and one species from the Antarctic (*B. hamiltoni*) have not been seen by the writer.

Records of extensive collections of *Bolbosoma* from North America have not found their way into the literature. This statement is borne out by the fact that Meyer (1933:395) in listing the species of Acanthocephala by continents does not record any species of *Bolbosoma* from North or Central America. Except for some doubtful species mentioned in the early literature as from intermediate hosts, the present study has brought forth evidence of only two species of *Bolbosoma* found in whales taken in waters off the coast of North America. These are *B. balanae* and *B. vasculosum*. In the special literature there is evidence (Meyer, 1931b, 1932; Baylis, 1932; *et al.*) that several of the species of *Bolbosoma* are widely distributed in the north Atlantic and the Mediterranean while the same species have been reported from New Zealand and islands of the Antarctic. Since the whale hosts are also wide ranging,

and migratory, it seems probable that most of the species of *Bolbosoma* are not distinctively limited in their geographical distribution similar to that which has been demonstrated for some members of the genus *Corynosoma* living in seals and other marine mammals.

The scanty material of *Bolbosoma* recorded for North America is probably attributable to the fact that the internal parasites of a mammal the size of a whale are not easily obtained. The interminable lengths of intestine that would have to be opened and searched would in itself be a potent deterrent to the intentions of most collectors. Furthermore, most of the whales that are killed are taken because of their commercial value and the dispatch with which the carcasses and viscera are converted into oil and commercial fertilizer leaves little opportunity for autopsy in the cause of pure science.

The writer feels confident that the treatment of the genus *Bolbosoma* as here presented must be regarded as but a preliminary study, not fully representative of the fauna as it occurs on this continent.

Description of the Species of Bolbosoma from North America.—

***Bolbosoma balanae* (Gmelin, 1790)**

(Plate 8, Figs. 73 and 74)

Synonyms: *Sipunculus lendix* Phipps, 1774, in part.

Echinorhynchus balanae Gmelin, 1790.

Echinorhynchus porrigens Rudolphi, 1819, of various authors.

Bolborhynchus porrigens (Rudolphi, 1819), of Porta, 1906.

Bolbosoma porrigens (Rudolphi, 1819), of Porta, 1908.

This species contains the largest individuals of *Bolbosoma* that have ever been recorded. Because of the large size it is not surprising that this was the first representative of the genus recognized in the intestine of whales. However, there has been much confusion in the literature regarding the name to be applied to this species because there have been so few definite morphological observations in the literature on this species down to the present generation. Much of the diagnosis which follows is taken from Meyer (1932).

DIAGNOSIS.—Adults reach a length of 190 to 205 mm and a diameter of 4 to 6 mm. The trunk of preserved individuals is in the form of a long, heavy cylinder with modifications at the anterior extremity. The anterior end of the trunk is expanded as a bulb about 7 mm wide by 8 mm long. This bulb has the form, in most individuals, of two cones placed base to base, the proximal one about 5 mm long and the distal cone slightly more than 3 mm. In some instances the distal cone may be partially retracted as a depression within the other part of the bulb. Usually the anterior cone of the trunk bulb is furnished with large, flat cuticular spines. The proximal cone is attached to the cylindrical hind-trunk by an attenuated region, considerably reduced, to a diameter of 1 or 2 mm.

This attenuated region is of variable length. According to Meyer (1932, fig. 63) the region of reduced diameter is about one-seventh of the entire length of the trunk, with its diameter expanding gradually to meet the full width of the trunk. In some specimens the constricted region is much more restricted and is sharply set off, abruptly, from the hind-trunk. The short praesoma, borne at the anterior end of the trunk cone, consists of a short neck in the form of a truncated cone and a conical proboscis about 1 mm long. The proboscis hooks are arranged as twenty-four longitudinal rows of 8 hooks each of which the basal one or two of each row is much smaller than the others.

Intermediate hosts in North America unknown.

Definitive host in North America an undetermined species of "whale," taken at Seattle, Washington, April 1, 1918, in collection U.S. Dept. Agr. No. 18784 (VC 2674).

In all of the current descriptions, the anterior region of the trunk bulb is described as set with cross rows of large spines. However, in two lots of specimens of this species examined by the present writer no bulb spines could be detected. At first this was regarded as possibly due to loss of the entire cuticular layer, due to rough handling of the material. However, one preserved specimen was available in which the bulb was intact, still embedded in the host tissue. This seemed to offer the opportunity to make a critical study of the bulb. The host tissue was carefully dissected away from the bulb. Then both the bulb and the surrounding tissues were stained and mounted for microscopic study. There is no evidence of spines on either the bulb or in the host tissue.

The writer is hesitant to suggest that bulb spines in individuals of *Bolbosoma* may ultimately disappear but the material at hand seems to fit the concept of *B. balanae* in every other respect. Furthermore, spination of the trunk bulb has been commonly regarded as an essential feature in the diagnosis of the genus *Bolbosoma*. Nothing but confusion could arise from recognition of a distinct genus for individuals lacking bulb spines and yet the solution of the current problem has not advanced to a point where an emendation of the generic concept seems warranted. The situation is similar to that found in *Corynosoma* wherein genital spines had been regarded as an essential feature of the genus but in some species they are lacking in one or the other of the two sexes and in some species they have been reported as entirely lacking in both sexes. In *Corynosoma*, functional mutilation results in removal of the genital spines of the females of some species and normal functional operation of the posterior extremity of the body in many species results in withdrawal of the genital spines into an introverted genital vestibule where they are completely obscured. Details of conditions in *Corynosoma* regarding the genital spines as a taxonomic feature have been advanced much fur-

ther than information about trunk bulb spines in the genus *Bolbosoma*. Further studies will need to be made before any recommendation regarding emendation of characterizations of either the genus or any of its species should be offered.

***Bolbosoma vasculosum* (Rudolphi, 1819)**

(Plate 8, Figs. 75 and 76)

Synonyms: *Echinorhynchus vasculosus* Rudolphi, 1819.

Echinorhynchus aurantiacus Risso, 1826.

Bolbosoma aurantiacum (Risso, 1826).

Echinorhynchus pellucidus Leuckart, 1828.

Echinorhynchus annulatus Molin, 1858.

Echinorhynchus serrani Linton, 1891.

Echinorhynchus bifasciatus Luehe, 1904.

The concept for this species has been very much in dispute. Founded on immature individuals more than a century ago, mature specimens have never yet been recorded.

DIAGNOSIS.—Body 12 to 15 mm long by 0.5 to 0.8 mm wide. Trunk bulb not conspicuously developed, about 1 mm long by 1 mm wide, shape that of an enlarged band rather than a definite bulb. Neck conical, three-fourths to 1 mm long. Proboscis subcylindrical, 0.76 to 1.00 mm long by 0.400 to 0.475 mm wide, with a slight enlargement near its middle. Hooks arranged in 18 to 20 longitudinal rows of 8 or 9 hooks each. Lemnisci about 1.5 mm long; Meyer (1932) cited them as 33.0 mm but by applying the scale of magnification to his drawing it is evident that this measurement is in error, possibly due to a misplaced decimal point. Largest hooks about 0.105 mm long, heavy, about 0.040 to 0.044 mm wide in lateral view where thorn and root meet; only about 0.024 mm wide when seen in face view of hook. Basal hooks about 0.079 mm long by 0.016 mm thick at base. Trunk spines in two separate collars or spine fields, the one on the largest part of the bulb about 0.048 mm long by about 0.020 mm wide; those of the anterior field shorter and narrower.

No fully mature individuals containing developing embryos have ever been recorded.

Only record for North America, the digestive tract of *Mesoplodon bidens* (*M. sowerbiensis*), Sowerby's beaked whale, collected by Cooper Curtice and deposited in the United States Department of Agriculture collections, accession no. 6326. This is the material which Leidy (1890) identified as *E. pellucidus* and was later named *B. aurantiacum* by Van Cleave (1925). According to Meyer (1932) both of these names are regarded as synonyms of *B. vasculosum*.

In Europe, late larvae of *B. vasculosum* have been recorded from various fishes of the Atlantic and Mediterranean oceans but an apparently

later stage, still immature, is reported from *Delphinus delphis*, the common dolphin of the Mediterranean.

In the more than a century since this species was described, the fact that no sexually mature individuals have been encountered in any collection makes it seem possible that the normal definitive host has never yet been found. Essential morphological features of this species seem to exclude the possibility that *B. vasculosum* might be the immature stage of one of the species which reach maturity in various whales.

XIII. COLLECTIONS OF ARCHIACANTHOCEPHALA FROM NORTH AMERICAN MAMMALS

Previous Studies.—As pointed out earlier in this monograph, the Archiacanthocephala are predominantly the parasites of the higher vertebrates, the birds and mammals. However, this fauna is poorly represented in the mammals of North America. Except for the parasites of a few species of mammals that have economic importance or significance in the health of man and his domestic animals, the Acanthocephala that occur as adults in land mammals of this continent have been but little investigated. Especially through the work of state and federal experiment stations there have been numerous collections of *Macracanthorhynchus* taken from the hog and brought together in museums and laboratories throughout the country. Many surveys have likewise been conducted to determine the presence or absence of *Moniliformis* in rats and other mammals. Most of the other genera of Archiacanthocephala are, as explained in Section VIII of this publication, found in restricted host relationships and commonly in very limited geographical areas. The distribution of some of the species in this last group must be regarded as but a fringe of the normal distribution extending from the more characteristic habitats in Central and South America into the southern borders of the United States. Collection of these invading forms has been a major project of only a few North American helminthologists. Numerous individuals have been active in local areas, especially in the southwestern states, and to several of these the writer is indebted for much of the material on Archiacanthocephala which forms the basis for the studies in the following section.

Generally speaking, there have been no prolonged programs of investigation of the Acanthocephala of land mammals of this continent comparable to those on marine mammals that are being conducted at the present time. The very early investigations of the acanthocephalan parasites of fishes and of birds, pursued by Leidy, Linton, and their contemporaries, yielded results which were tangible enough to inspire helminthologists of subsequent generations to follow up the researches on these parasites as new geographical frontiers were opened. In contrast, the discovery of Archiacanthocephala in land mammals of this continent has but rarely offered any commensurate return for efforts expended in other localities. As a consequence, some of the most distinctive parasites have re-

mained poorly understood. Thus, Leidy (1850) described a new species of acanthocephalan (*Hamanniella tortuosa*) from the intestine of the highly characteristic and widely distributed North American marsupial, *Didelphis virginiana* and although recent evidence indicates wide geographical distribution of the parasite it was not again mentioned in the literature until 1921.

In recent years a number of laboratories and of individuals have pursued comprehensive local surveys of the parasites of mammals. Often the chief tangible result of such a program has been the charting of new records of geographical distribution for the parasites, with only occasionally the discovery of distinctively new material. In some instances the discovery of widely isolated foci of infection remains unexplained as to whether they represent discontinuous distribution or the possibility that intervening regions have been inadequately investigated. Thus *Macracanthorhynchus ingens* has been found in Texas and in Pennsylvania but not in the broad expanse between these two areas although the definitive host, the raccoon (*Procyon lotor*), is well known throughout that territory. In this instance it seems probable that the sampling has been inadequate.

As a net result, the surveys so far completed have not added a single genus of mammalian Archiacanthocephala restricted to land mammals of North America as definitive host. At least two of the species most commonly encountered (*Macracanthorhynchus hirudinaceus* and *Moniliformis moniliformis*) are virtually cosmopolitan in their distribution, with only the presence of suitable definitive and intermediate hosts determining the ultimate pattern of local distribution. Several of the genera represented sparsely in the mammals of North America are but direct extensions of the fauna characteristic of Central and South America. The extent to which these incursions seem to be restricted to our southern border suggests that the migration northward is of relatively recent origin.

It has been pointed out in the discussion of the Palaeacanthocephala that many species have become continuously distributed through the Arctic and now occur in both the eastern and western hemispheres. However, for the Acanthocephala of land mammals there is no direct evidence that any species has made use of the passages between the two hemispheres to pass through the Arctic. This is in sharp contrast with the abundant evidence that several species of Archiacanthocephala have utilized the land connection as a one-way street from South to North America as their hosts have migrated northward.

XIV. ANALYSIS OF THE GENERA AND SPECIES OF THE FAMILY OLIGACANTHORHYNCHIDAE FOUND IN MAMMALS OF NORTH AMERICA

In the present investigation five genera of Oligacanthorhynchidae are recognized as normally utilizing North American mammals as definitive hosts. These are: *Macracanthorhynchus*, *Hamanniella*, *Oncicola*, *Pachysentis*, and *Echinopardalis*. In this section each of these genera will be treated historically, and a diagnosis of the genus will be presented along with a consideration of the species known to occur on this continent.

GENUS MACRACANTHORHYNCHUS Travassos, 1917a

Synonyms: *Echinorhynchus* Zoega in Mueller, 1776, in part.

Gigantorhynchus Hamann, 1892, in part.

Hormorhynchus Ward, 1917, of Johnston, 1918.

The giant thorny-headed worm of the hog is the most widely known species of the phylum Acanthocephala. This is attributable to the fact that it has attained practically cosmopolitan distribution through human agencies and the species is one of the few members of the phylum having direct economic importance. Although it is highly specialized, in zoological texts and in laboratories, it is commonly cited as a typical example of the phylum. Because of its availability, its large size, and its economic importance, the morphology, ontogeny, and physiology have been more intensively studied than they have for any other acanthocephalan.

The scientific name first attached to the typical representative of this genus was *Taenia hirudinacea*, because no one had recognized the thorny-headed worms as a distinct group when Pallas (1781) gave it a name which placed it among the tapeworms. Although the generic name *Echinorhynchus* had been introduced into the literature in the work of Mueller in 1776, it was not immediately applied to the worms from swine. Soon, however, the name *Echinorhynchus* became applied to all species of Acanthocephala and thereafter the form from the hog became known as *Echinorhynchus hirudinaceus* or by the more widely accepted name *Echinorhynchus gigas* which Bloch introduced in 1782. The species concept continued to go under the generic name *Echinorhynchus* until 1892 when Hamann took the first significant step toward recognition of families and genera within the Acanthocephala. Thereafter this species was very generally recognized as either *Gigantorhynchus gigas* or *Gi-*

gantorhynchus hirudinaceus until 1917a when Travassos proposed *Macracanthorhynchus* as a new generic name with *E. hirudinaceus* Pallas, 1781 as genotype.

In the literature, 1916 is very commonly cited as date for *Macracanthorhynchus* but that is the date on which the name was proposed in a paper for a scientific program (Van Cleave, 1952a). The name did not become available until 1917 when it was published along with a diagnosis.

Chiefly through the agency of man in transporting domestic swine to all parts of the earth, this genus has attained essentially cosmopolitan distribution. Adaptability to a wide variety of both definitive and first intermediate hosts has greatly facilitated the establishment of *M. hirudinaceus* in new territory where introduced.

Two other species, of limited distribution, have been assigned to the genus *Macracanthorhynchus*. Only one of these, *M. ingens*, is known from North America and this species is apparently restricted to this continent.

Diagnosis of Macracanthorhynchus.—With the characters of the family Oligacanthorhynchidae. Body large to very large, circular in cross section when preserved, usually tapering gradually from the anterior region of maximum diameter. Both ends somewhat flexed ventrally. Surface of mature females shallowly cross-furrowed in irregular pattern. Proboscis globular, with six spiral rows of six hooks each. Lemnisci flat, ribbon-like, with a few giant nuclei anteriorly. Male genital organs occupy more than half the length of the body; testes tandem, elongately elliptical, not contiguous. Eight ovoidal cement glands stretched in an elongate series, commonly paired laterally. Eggs with concentric membranes, the outer shell with net-like surface sculpturing. Parasitic as adults in mammals.

***Macracanthorhynchus hirudinaceus* (Pallas, 1781)**

(Text Figs. D to J; Plate 9, Figs. 77 to 82)

Synonyms: *Taenia hirudinacea* Pallas, 1781.

Taenia haeruca Pallas, 1766, in part.

Echinorhynchus hirudinaceus (Pallas, 1781).

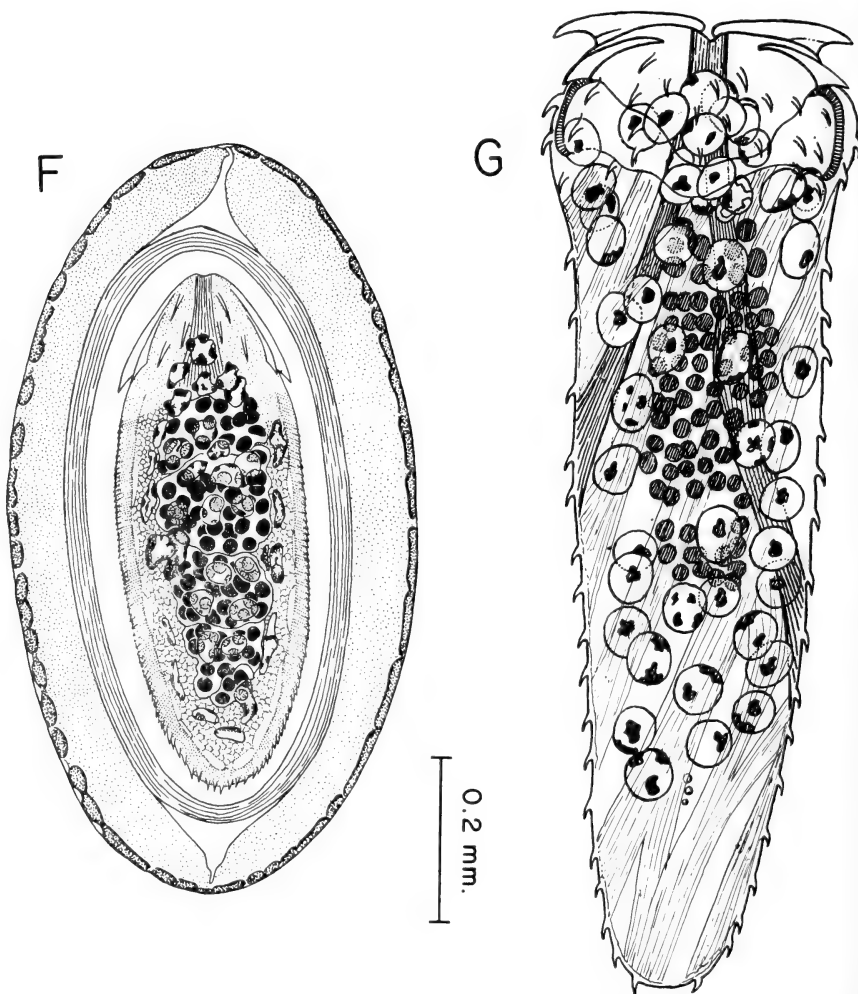
Gigantorhynchus hirudinaceus (Pallas, 1781).

Echinorhynchus gigas Bloch, 1782.

Gigantorhynchus gigas (Bloch, 1782).

Hormorhynchus gigas (Bloch, 1782), of Johnston, 1918.

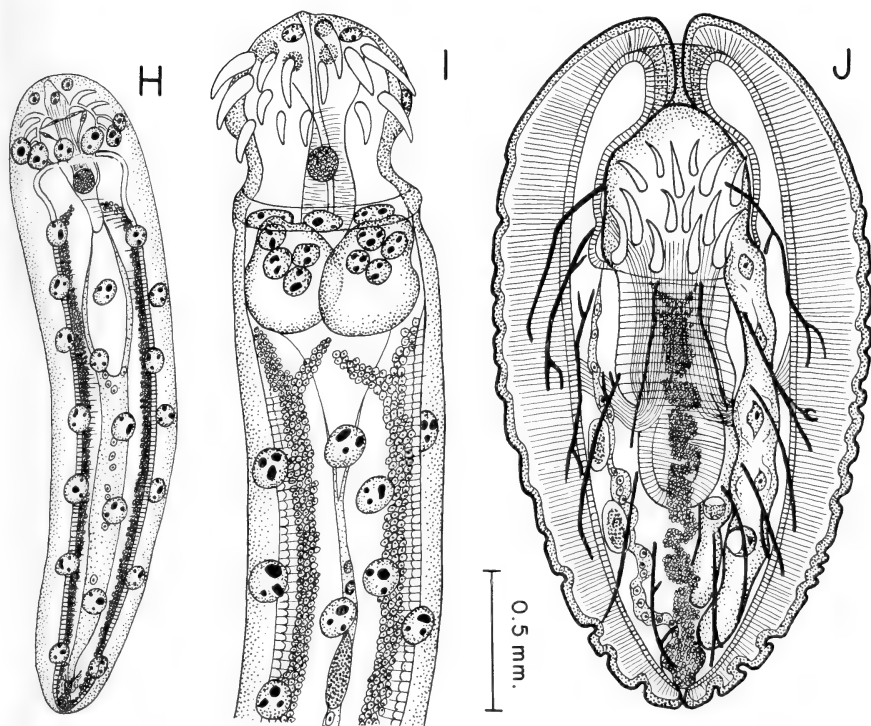
It is frequently true that some of the best-known species are poorly and incompletely described in the literature. This is due, at least in part, to the fact that forms which are regarded as common are presumed to be so easily recognized that no one considers it worth-while to offer a detailed description. Very few of the descriptions of *M. hirudinaceus* give measurements for the proboscis and many of the details are at variance in the writings of different authors. Meyer (1932) quotes from Travassos



TEXT FIGS. F AND G. Earliest stages in the ontogeny of *Macracanthorhynchus hirudinaceus*. (After Meyer.)

F. Fully embryonated hard-shelled embryo discharged from the body of a gravid female, showing the enveloping membranes enclosing the advanced larva practically ready for hatching.

G. Acanthor after liberation from embryonic membranes, taken from the body cavity of an insect intermediate host. The crown of penetration spines on the anterior extremity is a strictly larval structure, having no relationship to the adult proboscis. The body spines are likewise larval, lost later in development.



TEXT FIGS. H TO J. Later stages in the ontogeny of *Macracanthorhynchus hirudinaceus*. Note that these three drawings are at approximately uniform magnification but are at a scale different from Text Figs. F and G. (Redrawn from Kates, 1943.)

H. A fairly young acanthella, showing early stage in formation of the adult proboscis, most of other structures still rudimentary. The large, spheroidal nuclei later migrate to their definitive positions and transform in shape to condition characteristic of adult worm.

I. Anterior extremity of an advanced acanthella showing the proboscis approaching the definitive adult form. The two sacs dependent from the neck region, immediately posterior to the proboscis, are the rudiments of the lemnisci. Structures in the region of the body omitted from this drawing have not advanced materially over those shown in Text Fig. H.

J. Cystacanth or infective juvenile encysted in the tissues of a beetle larva. At this stage metamorphosis has been completed and all structures of the adult are present in miniature. The proboscis has been introverted into the proboscis receptacle and the entire praesoma has been retracted into the anterior end of the trunk. The body wall has been differentiated and greatly thickened and the subcuticular nuclei which were spheroidal in the acanthella stages before metamorphosis have become elongated and branched.

(1917b) with the statement that the proboscis of this species is 1.0 mm long and 0.5 mm in maximum width. It seems probable that these two measurements were transposed. Kaiser (1891:9) mentions the small proboscis which scarcely reaches the diameter of 1.0 mm. His statement is in keeping with observations of the present writer who has found that in this species the proboscis is very commonly about 0.9 mm in maximum diameter and only about 0.6 mm long.

In the closing decade of the nineteenth century, the general outline of the life history of *M. hirudinaceus* had been sketched but full cytological details of the ontogeny were not completely available until Meyer (1928, 1931c, 1934, 1935, 1936, 1937, 1938a, 1938b) published his memorable series of studies. In North America, the intermediate hosts were studied particularly by Glasgow (1926, 1927a, 1927b), and at a later date Kates carried on extensive experimental studies (1941, 1942, 1943, 1944).

DIAGNOSIS.—Body very large, in some females attaining 650 mm with a diameter of 7 or 8 mm near the anterior end of the trunk; males 50 to 90 mm long and 6 to 8 mm broad. Body of living worm, in normal habitat, flat but becoming turgid in water or preserving fluid. In both sexes the body tapers gradually from the region immediately posterior to the praesoma to a considerably smaller size near the posterior end. Old, fully grown females commonly showing shallow, irregular transverse wrinkles; males usually lacking transverse folds. Both sexes usually with slight ventral bending of both extremities, some females showing tendency toward coiling. Proboscis globular, about 0.6 to 1.0 mm long by 0.50 to 0.92 mm in maximum width; with six spiral rows of six hooks each. Largest hooks (according to Travassos) 0.432 mm long; smallest, in basal circle, 0.260 mm from tip of thorn to anterior extremity of the anterior root. In some specimens from pigs of North America the hooks tend to be larger than the measurements given by Travassos, with some of the anterior hooks as much as 0.480 mm long. Lemnisci flat, ribbon-shaped, 20 to 35 mm long, broadened posteriorly; each with 6 giant nuclei (occasionally 5 or 7). Testes located in front half of body; eight elliptical cement glands often arranged in pairs as an elongated series. Protonephridial excretory organs associated with genital tract of both sexes. Mature embryos within gravid females 0.092 to 0.100 mm long by 0.051 to 0.056 mm wide.

Definitive hosts: in North America domestic swine (*Sus scrofa domestica*), fox squirrels (*Sciurus niger rufiventer* and *S. niger niger*). Immature individuals in intestine of *Scalopus aquaticus*, collected by H. E. Essex in Illinois and *Tamias striatus fisheri* taken in Ohio by R. L. Rausch.

First intermediate hosts: Moore (1946) states that more than 25 species of beetle larvae (mostly scarabaeids) serve as intermediate hosts of

M. hirudinaceus. There is apparently little restriction as to larval hosts, almost any soil inhabiting beetle larva being capable of serving this species and in some instances it has been demonstrated that cystacanths remained infective in the bodies of transformed adult beetles (Glasgow, 1926). In North America the following have been proved capable of serving as first intermediate hosts: *Phyllophaga vehemens*, *P. rugosa*, *Cotinis nitida*, *Xyloryctes satyrus* and many other June beetle larvae and adults. *Strategus julianus*, which as a larva develops in rotting logs, has been infected experimentally (Manter, 1928).

Glasgow and De Porte (1940) have demonstrated that viable eggs of *M. hirudinaceus* may be recovered from the droppings of domestic pigeons and report that eggs may be carried on the feet of various birds. In their capacity as mechanical vectors, birds probably have an important role in the widespread distribution of the giant thorny-headed worm of hogs.

MATERIAL OF *Macracanthorhynchus hirudinaceus* FROM MAMMALS OF NORTH AMERICA EXAMINED IN THIS STUDY.—

Host	Locality	Date	Collector	Accession number
<i>Sus scrofa domestica</i> *				
<i>Tamias striatus fisheri</i>	Marion Co., O.	June 17, 1944	R. Rausch	VC 3785
<i>Sciurus niger rufiventer</i>	Radnor, O.	Sept. 23, 1943	R. Rausch	VC 3851
<i>Scalopus aquaticus</i>	Urbana, Ill.	Oct. 24, 1924	H. E. Essex	VC 2110

***Macracanthorhynchus ingens* (von Linstow, 1879)**

(Plate 9, Figs. 83 and 84)

Synonyms: *Echinorhynchus ingens* von Linstow, 1879.

Prosthenorchis ingens (von Linstow, 1879) of Travassos, 1917.

Echinorhynchus ingens was very briefly described by von Linstow (1879) from the raccoon, *Procyon lotor*. Through the early period of reorganization of the specific adjustments of Acanthocephala, no one attempted to assign this species to any modern genus. It had not been encountered frequently and the morphological information available was insufficient for positive assignment. In 1917, Travassos (1917b) tentatively ascribed it to the genus *Prosthenorchis* (*sensu lato*) but he did not seem to have confidence in his decision. No one either confirmed or challenged this assignment until Meyer (1932), with a query as to the validity of his judgment, transferred the species to the genus *Macracanthorhynchus*. The ultimate proof of the justification for this act was delayed until 1946 when Moore amplified the description and through

* Specimens from the domestic pig have been examined in such quantities that it does not seem worth while to list the individual collections which are so widely spread over the continent as to give no indication of limits to the geographical distribution of the parasite.

details of morphology and of ontogeny was able to establish a close agreement in many points between *M. hirudinaceus* and *M. ingens*.

DIAGNOSIS.—Body of large size; mature females 183 to 300 mm long and 5 to 8 mm wide; mature males 130 to 150 mm long and 4 to 5 mm wide. Proboscis sub-globular, 0.52 to 0.60 mm long; 0.60 to 0.84 mm in maximum diameter; armed with six transverse or diagonal rows of six hooks each (a total of 36 hooks). In a series of specimens received through the courtesy of Dr. Moore, the measurements of proboscis hooks are entirely out of line with those cited by Moore (1946). The discrepancies are so pronounced that it seems very likely that in transcribing his measurements, Moore misplaced the decimal point. None of the specimens in the writer's collection shows the roots clearly, so measurements of the thorns alone will be given. The anteriormost thorn in each longitudinal row is from 0.127 to 0.150 mm long. Thorns of the second hook in each longitudinal series, designated as Type II by Moore, are from 0.104 to 0.115 mm. The basal hook in each longitudinal row is, as Moore states, devoid of prominent root and has a length of approximately 0.08 mm. The anterior hook in each longitudinal row is acuminate at the point while the second is chisel-like.

Elongate testes tandem in middle of body, about 11 mm apart. Eight cement glands ellipsoidal, with a tendency toward pairing. Mature eggs with concentric membranes, outer shell heavy, dark brown, irregularly grooved or ridged; 0.096 to 0.106 mm long by 0.051 to 0.054 mm wide.

Definitive host: the raccoon (*Procyon lotor*) of the states of Texas and Pennsylvania (Chandler and Melvin, 1951).

Intermediate hosts: Moore (1946) has demonstrated experimentally that *M. ingens* in Texas will undergo its larval development in *Phyllophaga crinita* Burmeister, *P. hirtiventris* Horn and *Ligyris* sp. Moore also determined experimentally that a frog may be a possible transport host. In Pennsylvania, Chandler and Melvin (1951) found immature individuals in *Mustela vison*, *Mephitis mephitis nigra*, *Urocyon cinereoargenteus* and *Parascalops breweri*.

It is thought that the apparent discontinuous distribution of *M. ingens* is due to incomplete records of its occurrence in intervening states.

MATERIAL OF *Macracanthorhynchus ingens* EXAMINED IN THIS STUDY.—

Host	Locality	Date	Collector	Accession number
<i>Procyon lotor</i>	Texas	1942	H. L. Van Volkenberg	VC 3807
<i>Procyon lotor</i>	Texas	?	D. V. Moore	VC 3816
<i>Procyon lotor</i>	Angelina Co., Tex.	?	D. V. Moore	VC 4132

GENUS HAMANNIELLA Travassos, 1915b

Synonyms: *Echinorhynchus* Zoega, in Mueller, 1776, in part.
Gigantorhynchus Hamann, 1892, in part.

Hamania Neiva, 1915.

Hamania Travassos, 1915a.

Hamannia Travassos, 1915a, *nec* Railliet, Henry, and Sisoff, 1912.

Hamaniella Travassos, 1915b.

Mamanniella Travassos, 1917c, typographical error.

Travassosia Meyer, 1931, *nom. nud.*

Travassosia Meyer, 1932.

This is a genus for which available records indicate that all the species are restricted to the Americas. *Echinorhynchus microcephalus* Rudolphi, 1819, was cited as type of the genus *Hamania* in an article in the *Brazil-Medico* (Vol. 29, No. 12, p. 89) with the authorship of the article clearly attributed to Arthur Neiva. However, in a later issue of the same volume (Vol. 29, No. 14, p. 105) the article was reprinted in full with the authorship corrected to Lauro Travassos. In both of these references the name of the genus was given as "*Hamania*," although it was obviously intended as a patronym honoring Dr. Otto Hamann. In the same year, Travassos (1915b, *Brazil-Medico* 29 (18):137) recognized the fact that the intended name had been preoccupied by Railliet, Henry, and Sisoff (1912) for a subgenus of nematodes. Thereupon Travassos (1915b, *Brazil-Medico* 29 (18):137) proposed an entirely new name, "*Hamaniella*," for his acanthocephalan genus, persisting in the misspelling, although in that new reference he seemed to have regarded the original spelling of "*Hamania*" as merely a typographical error. Without calling particular attention to the change, Travassos (1917b, *Mem. Inst. Oswaldo Cruz* 9 (1):37) finally corrected the spelling to "*Hamanniella*" but later in the same monograph (page 40) he lapsed into the erroneous spelling again.

In 1917, Travassos described *Hamaniella carinii* (1917a) as a new species from South American armadillos. On what is now regarded as insufficient evidence, Meyer, 1932, decided that this species is generically distinct from *Hamanniella* and in consequence he erected a new generic concept to which he applied the new name *Travassosia*. Meyer (1931a), when he outlined the broad revision of the families and genera of Acanthocephala, listed several new genera which he defined and gave status in that same publication. However, among the new names presented under the Archiacanthocephala he included parenthetically (Gen. *Travassosia*, n.g.) but he made no further mention of the genus, gave no diagnosis and cited no species in the 1931 publication. He thus clearly indicated uncertainty as to the validity of *Travassosia*. However, in the detailed monograph (1932:203) he revived the name, using the following heading in the list of Oligacanthorhynchidae: "4. Genus *Travassosia* nom. nov. (Meyer 1931)." As of 1931, that name is a *nomen nudum* and has no validity in the literature. Furthermore, Meyer was in error when he designated the name as a "new name" because he based the generic concept upon *Hamanniella carinii* of Travassos and under the International Rules

of Nomenclature the new concept, if valid, is a new genus, not a new name. For a time the present writer accepted this decision of Meyer and in 1947 described as *Travassosia tumida*, a new species from an armadillo of North America. A later evaluation of the presumed generic characters and distinctions between *Hamanniella* and *Travassosia* led the writer to alter his opinion and to declare *Travassosia* as a direct synonym of *Hamanniella* (present monograph).

Van Cleave (1925), in reviewing the works of Leidy, concluded that *Echinorhynchus tortuosus* Leidy, 1850 is ascribable to the genus *Hamanniella*. Thus as at present constituted *Hamanniella* includes two species from South American and two from North American mammals.

Diagnosis of Hamanniella.—With the characters of the family Oligacanthorhynchidae. Body large, cylindrical when preserved, often somewhat spirally coiled; the anterior extremity much reduced in diameter; surface with strong cross-foldings which in some species impart a ruffled appearance of the lateral surfaces. Proboscis globular, with six spiral rows of six hooks each or otherwise expressible as twelve longitudinal rows of three hooks each. Largest hooks bear relatively heavy roots, some of which have the anteriorly directed root bifurcated. Lemnisci cylindrical, very long, at times reaching 15 mm, with large nuclei. Male reproductive organs in posterior half of body; testes ellipsoidal, considerable distance from each other; eight cement glands ovoidal to ellipsoidal, irregularly arranged in a relatively short series.

Parasites of mammals of the western hemisphere. Two species known from North America.

Type of genus, *Echinorhynchus microcephalus* Rudolphi, 1819.

***Hamanniella tortuosa* (Leidy, 1850)**

(Plate 10, Figs. 85 to 90)

Synonym: *Echinorhynchus tortuosus* Leidy, 1850.

This species was first named by Leidy (1850) from an immature specimen which had perforated the intestinal wall of the opossum and had the anterior part of its body buried in an oval mesenterial "tumor." Although the species appears to be not rare in America, the species was not mentioned again until Van Cleave (1921) redescribed it more fully on the basis of adult worms taken from the opossum (*Didelphis virginiana*) taken from Oklahoma and Texas. Subsequently there have been but few references to this species, among the most significant being those by Moore, 1942, and by Chandler, 1946, 1947. In the meantime considerable numbers of collections have accumulated in the study series of the writer.

DIAGNOSIS.—With the characters of the genus *Hamanniella*. Body large, long, heavy, circular in cross section when preserved; cross furrows tend-

ing to produce a ruffled appearance in body wall radiating from the ventral surface. The anterior extremity much reduced in diameter and usually lacking cross furrows. Females to about 220 mm long by 8 mm in maximum diameter. Males about 100 mm long by 3 mm in maximum diameter. Proboscis globular, approximately 0.22 to 0.23 mm long by 0.23 to 0.29 mm in maximum diameter (Van Cleave, 1921, erroneously recorded the length of the entire praesoma as proboscis length and Meyer, 1932, copied this error). Proboscis hooks arranged in 12 longitudinal rows of 3 hooks each, but rows not always in perfect alignment. This is the equivalent of the 6 spiral rows of 6 hooks each (see Text Fig. C) as cited for this genus by Meyer. Largest hooks 0.079 to 0.105 mm long from tip of thorn to anterior end of anterior root; hooks near middle of proboscis about 0.082 mm long; basal hooks vary from 0.040 to 0.059 mm in length. Lemnisci often attaining a length of 14 mm. Male organs confined to posterior half of body, testes elongately ellipsoidal, each approximately 4 to 5 mm long by about 1.25 mm wide; the two widely separated from each other. Testes followed, but not immediately, by 8 cement glands. Mature embryos within body cavity of gravid females 0.082 to 0.118 mm long by 0.035 to 0.590 mm broad, membranes essentially concentric.

MATERIAL OF *Hamanniella tortuosa* FROM MAMMALS OF NORTH AMERICA EXAMINED IN THIS STUDY.—

Host	Locality	Date	Collector	Accession number
<i>Didelphis virginiana</i>	Louisiana	R. Combs	VC 2174
<i>Didelphis virginiana</i>	Idabel, Okla.	Sept. 1, 1910	H. Douthitt	VC 2223
<i>Didelphis virginiana</i>	College Sta., Tex.	VC 2224
<i>Didelphis virginiana</i>	Houston, Tex.	Jan., 1946	A. C. Chandler	VC 4088
<i>Didelphis virginiana</i>	So. Miami, Fla.	May 12, 1949	W. H. Leigh	VC 4315

***Hamanniella tumida* (Van Cleave, 1947a)**

(Plate 10, Figs. 91 to 95)

Synonym: *Travassosia tumida* Van Cleave, 1947.

In 1947, the writer described a new species of acanthocephalan from the opossum (*Didelphis virginiana virginiana* Kerr) of near Fort Sill, Oklahoma. In most details this material was in agreement with the diagnosis of the genus *Travassosia* which Meyer suggested in 1931 and validated by publication of a description in 1932. As pointed out elsewhere in the present publication, it has been shown that *Travassosia* is a direct synonym of *Hamanniella*, and hence the species from North America is here described as *Hamanniella tumida* (Van Cleave, 1947a).

DIAGNOSIS.—With the characteristics of the genus *Hamanniella* as emended in the present monograph. Body very long, relatively large, smooth except for very slight cross wrinkling of the rapidly tapering

trunk toward the praesoma. Body wall very thin, musculature relatively weak, females 100 to 238 mm long, males 74 to 115 mm. Bodies of preserved specimens circular in cross section; females before compressing for making stained whole mounts, 3 to 6 mm in maximum diameter; males 1.5 to 2.0 mm. Attenuated trunk region immediately posterior to praesoma of females 0.27 to 0.35 mm in diameter, of males 0.27 to 0.31 mm. Praesoma about 0.38 to 0.57 mm in length. Proboscis short, approaching globular, with breadth and length almost identical in most individuals, in females measuring 0.230 to 0.312 mm in length and breadth; in males 0.210 to 0.289 mm. Proboscis armature consisting of 6 spiral rows with 6 relatively strong hooks in each row, each provided with one or more root processes. Root processes of anterior two hooks in each row with a long, anteriorly directed extension in addition to a short posterior process; at least in some individuals the anterior process is cleft, Y-shaped. Roots of the remaining hooks are broad, of irregular shape. Many of the larger hooks have a lance-like or arrow-head shaped point. The larger hooks often attain a diameter of from 0.026 to 0.029 mm at the bend where blade and root meet. Anteriormost hooks from 0.100 to 0.130 mm in length from tip to anterior end of root, with the root having an over-all length of 0.079 to 0.084 mm. Second hooks in each series somewhat smaller in diameter but longer than the first hook (because the anterior projection of the root is longer), sometimes attaining a length of 0.150 mm; over-all length of roots 0.093 to 0.099 mm. The fourth root in each series, the first lacking anterior and posterior prolongations of the root, is 0.065 to 0.079 mm long. Basal hooks seen in side view, relatively small, 0.045 to 0.065 mm in length. Lemnisci very long, cylindrical, with a central canal; usually much looped; in some individuals reach a length of 15 mm with diameter of 0.130 to 0.175 mm; nuclei of lemnisci few in number, in some instances as much as 0.5 mm long with diameter of 0.058 mm. Protonephridial organs not recognized in the available material.

Male genitalia occupy from one-third to two-fifths of the posterior region of the body cavity. Testes long, ellipsoidal, far removed one from the other, often each about 5 mm long. Cement glands 8, somewhat irregularly paired, extending as a series for a distance of about 5.7 mm, the largest about 2.5 mm long. Copulatory bursa, when extruded, long and narrow.

Vagina and uterus of female, prominent, muscular, in characteristically flexed position, the uterine bell of the selective apparatus showing definite attachment with the ligament sacs. Female genital aperture almost terminal. Eggs within ligament sacs and uterus 0.090 to 0.098 mm long by 0.040 to 0.048 mm in width. Developmental stages and intermediate hosts wholly unknown.

Definitive host: *Didelphis virginiana virginiana* (opossum), the only species on record.

GENUS *ONCICOLA* Travassos, 1917a

Synonym: *Echinorhynchus* Zoega in Mueller, 1776, in part.

This genus is restricted to carnivores as normal definitive hosts. Travassos was the first to recognize the concept but the history of the name is surrounded by error and ambiguity even greater than that attached to the genus *Macracanthorhynchus*. Travassos claimed that the name dated from 1916 but that was the date on which it was presented on a program and the name was not published until 1917 (Van Cleave, 1952a). Because of the obscure place of publication the name did not get into American and European publications for some time. Thus Stiles and Hassall, as late as 1920, did not include *Oncicola* in the *Index-Catalogue of Roundworms* and Schulze omitted reference to it in his *Nomenclator*. The name finally was entered in the *Zoological Record* for 1929 on the basis of its occurrence in the *Memorias Instituto Oswaldo Cruz* (Travassos, 1917b) but in the following issue of *Zoological Record* the date was changed to 1916, as quoted by Travassos, although the editors of the *Record* used the symbol "n.v." to indicate that they had not seen the publication of that presumed date.

The genus seems to have become established in the faunas of South and North America, Africa, Palestine, and some of the islands of the south Pacific.

A single species, *Oncicola canis* (Kaupp, 1909) is known from carnivores of North America. In the present publication this species is reported from domestic cats and from a lynx for the first time, all previous records for North America having been from domestic dog and coyote as definitive hosts.

Diagnosis of Oncicola.—With the characters of the family Oligacanthorhynchidae. Body relatively small, short, fairly thickset. Neck short, often invaginated around base of the proboscis. Proboscis globular, armed with six diagonal rows of six hooks each, roots of hooks not conspicuously asymmetrical. Lemnisci long, cylindrical. Male reproductive organs extending into anterior half of body, testes contiguous or partially overlapping, eight cement glands ovoidal to elongate, in immediate contact with posterior testes. Protonephridial organs present. Mature eggs broadly ellipsoidal, without especially compact external shell.

Type of the genus, *Oncicola onicola* (von Ihering, 1902) Travassos, 1917a.

Oncicola canis (Kaupp, 1909)

(Plate 10, Figs. 96 and 97)

Synonyms: *Echinorhynchus canis* Kaupp, 1909.*Echinorhynchus* sp.? Ward, 1897.*Gigantorhynchus canis* (Kaupp, 1909) of Hall and Wigdor, 1918.

Ward (1897) recorded the occurrence of *Echinorhynchus* sp.? in dogs of Lincoln, Nebraska. Van Cleave (1921) re-examined the original material on which this record was based and identified the acanthocephalan as *Oncicola canis* (Kaupp, 1909). There have been only a few scattered references to this species in the literature. Parker, who discovered the species in the intestine of a dog at San Antonio, Texas, published a brief account (1909) of the reactions of the infected dog. According to his observation, the dog, which carried about 300 specimens of *O. canis*, died of symptoms strongly indicative of rabies, but autopsy revealed only the acanthocephalans as the presumed cause of the disorder. This observation calls to mind the early account of Grassi and Calandruccio (1888) in which they described the discomfort experienced following a self-imposed infection with *Moniliformis moniliformis*.

Hall and Wigdor (1918) attributed *E. canis* to the genus *Oncicola* but in the same article all of the descriptions of drawings referred to this species as *Gigantorhynchus canis* (Kaupp, 1909). Van Cleave (1921) identified acanthocephalans from mesenteric cysts of an armadillo (*Dasypus novemcinctus texanus*) as the immature individuals of *O. canis*. Recent re-examination of some of that material reveals the presence of strongly developed, asymmetrical roots on the larger hooks of the proboscis indicating that at least some of the encysted worms might belong to the genus *Echinopardalis*. The ease with which these two genera may be confused is illustrated in the work of Witenberg (1938) who declared that Meyer (1931a) described the identical species under the two names *Oncicola macrurae* and *Echinopardalis macrurae*.

Price (1928) found *O. canis* in the coyote of Eagle Pass, Texas. The following year (1929) Price recorded the occurrence of larval worms in esophageal cysts of turkey poults at San Angelo, Texas. It seems obvious that these worms from the turkey must represent an accidental infection.

Chandler (1946), on the basis of finding a high percentage of dead worms in mesenteric cysts of the armadillo, suggested that the armadillo is a possible means of destroying infected intermediate hosts rather than serving as an essential transport host through which carnivores become infected. The untenable nature of this argument is evident when it is recalled that dead larvae of other groups of parasitic worms are often found in calcified cysts within normal intermediate hosts. Although it has been demonstrated frequently that there is rarely rigid specificity for intermediate hosts of Archiacanthocephala, Chandler (1946) re-

marked on the fact that *Oncicola* occurs in Africa and other regions where there are no armadillos.

The present report contains the first records of the occurrence of *Oncicola* in Felidae of North America. This host relationship is in keeping with the records of species of the genus from South America where Felidae are commonly the hosts of representatives of the genus *Oncicola*.

DIAGNOSIS.—With the characteristics of the genus *Oncicola*. Body short and heavy, with irregular cross furrows; 6 to 14 mm long, some fully mature females as much as 4 mm in maximum width near the anterior end of the trunk. Proboscis globular, 0.37 to 0.46 mm long by 0.4 to 0.5 mm in diameter. Hooks arranged in six spiral rows of six hooks each. Largest hooks greatly curved, roots not clearly differentiated in available specimens but conspicuously developed. Largest thorns about 0.067 mm long, those at base of proboscis about 0.530 mm. Male organs occupy more than one-half the length of the body cavity; testes contiguous; cement glands 8, ovoidal or pyriform. Eggs in body cavity of mature female about 0.081 by 0.046 mm, membranes concentric.

MATERIAL OF *Oncicola canis* FROM NORTH AMERICAN MAMMALS EXAMINED IN THIS STUDY.—

Host	Locality	Date	Collector	Accession number
<i>Canis familiaris</i>	San Antonio, Tex.	1909	J. W. Parker	VC 2225
<i>Canis familiaris</i>	Lufkin, Tex.	Mar. 25, 1926	E. W. Price	VC 2347
<i>Canis familiaris</i>	Lincoln, Nebr.	1897	H. B. Ward	VC 2614
<i>Canis latrans</i>	Central Texas	1942	H. L. Van Volkenberg	VC 3808
<i>Canis latrans</i>	Moran, Wyo.	June 26, 1948	R. Rausch	VC 4144
<i>Lynx rufus</i>	Arizona	C. A. Hannum	VC 3632
<i>Felis domestica</i>	Washington, D.C.	Kilbourne	VC 2646
<i>Felis domestica</i>	?	?	B. A. I. 3728	VC 4062
<i>Felis domestica</i>	Illinois?	?	A. R. Cooper	VC 1725
<i>Felis domestica</i>	Austin, Tex.	1951	C. W. Deslandes	VC 4487
<i>Immature</i>				
<i>Dasypus novemcinctus texanus</i>	Texas	1891	A. Hassall	VC 1657

GENUS PACHYSENTIS Meyer, 1931a

The genus *Pachysentis* was proposed by Meyer (1931a) to include three species of relatively large, plump, *Acanthocephala* from carnivores of Brazil and Egypt. In the original characterization, the members of this genus are distinguishable from other *Archiacanthocephala* on the basis of the number of spiral rows of proboscis hooks. This feature is not regarded by the present writer as sufficient basis for setting apart this genus to a distinct family as proposed by Meyer. Elsewhere in the present monograph the name *Pachysentidae* is regarded as a direct synonym for the family *Oligacanthorhynchidae*. In some members of the

genus *Pachysentis* the twelve spiral rows of proboscis hooks are readily distinguishable from the six spiral rows distinctive for the other genera of the Oligacanthorhynchidae. In all instances, the hook formula exceeds the six spiral rows of six hooks each distinctive of most other genera of Oligacanthorhynchidae.

Diagnosis of Pachysentis.—With the characteristics of the family Oligacanthorhynchidae as emended in the present publication. Body fairly large, relatively thickset. Proboscis approximately globular, with more than 36 hooks, often not arranged in perfect rows but in some instances in 12 spiral rows of six hooks each. Hooks more crowded on the basal portion of the proboscis than on anterior region. Anterior hooks with both anterior and posterior roots. With protonephridial excretory organs. Lemnisci elongated, flattened, with a few large nuclei. Parasitic as adults in the intestines of carnivores.

The writer has not been able to find any evidence that a genotype has ever been designated for the genus *Pachysentis*. *Pachysentis canicola* Meyer, 1931a, is hereby designated as type of the genus.

***Pachysentis canicola* (Meyer, 1931a)**

(Plate 11, Figs. 99 to 107; Plate 12, Figs. 114 to 116)

Meyer (1931a) described this species from unnamed specimens in the Berlin Museum which Olfers and Sello collected from an undetermined species of "Canis" in Brazil. The life history of the species is wholly unknown.

H. K. Buechner (1944) was the first to record the presence of a representative of the genus *Pachysentis* in North America. According to his report, he found *P. canicola* in the gray fox, *Urocyon cinereoargenteus scotti*, of Texas. The present writer has had material from the same host from Texas, supplied by Buechner and by Van Volkenberg, and in addition has had the privilege of studying materials of *Pachysentis* from various species of skunk collected by Jack Tiner in Texas. One series of collections from *Mephitis* sp. was taken by F. McMurray from Cache, Oklahoma. Although there seems to be considerable individual variability within these series of collections, all seem to be attributable to *P. canicola* Meyer.

DIAGNOSIS.—With the characters of the genus *Pachysentis*. Body relatively short and heavy, greatest diameter near the middle or in anterior third. Females 20 to 26 mm long by 5 to 11 mm in maximum diameter. Males 15 to 28 mm long by 4 to 8 mm in maximum diameter. Proboscis globular, 0.57 to 0.80 mm long by approximately the same maximum width. Hooks not always in perfect rows. Sometimes in twelve diagonal spirals of six hooks each, of which only the anterior 3 or 4 have promi-

nent roots. Longest hooks 0.173 to 0.346 mm long from tip of thorn to anterior extremity of anteriorly directed root. Testes elongate ellipsoidal, in contact with each other. Eight cement glands ovoidal. Mature embryos in body of gravid female 0.058 to 0.072 mm long by 0.038 to 0.045 mm wide, membranes concentric.

MATERIAL OF *Pachysentis canicola* EXAMINED IN THE PRESENT STUDY.—

Host	Locality	Date	Collector	Accession number
<i>Urocyon cinereo-argentatus scotti</i>	Central Texas	1942	H. K. Buechner	VC 3745
<i>Urocyon cinereo-argentatus scotti</i>	Central Texas	1942	H. K. Buechner and	
"Skunk"	Central Texas	1942	H. L. Van Volkenberg	VC 3757
<i>Mephitis mesomelas</i>	Central Texas	H. L. Van Volkenberg	VC 3810
<i>Conepatus mesoleucas</i>	Central Texas	J. Tiner	VC 3800
<i>Spilogale leucoparia</i>	Central Texas	J. Tiner	VC 3800
<i>Mephitis</i> sp.	Cache, Okla.	1940	J. Tiner	VC 3800
			F. McMurray	VC 3948

Intermediate hosts unknown for North America.

GENUS ECHINOPARDALIS Travassos, 1918

Synonyms: *Pardalis* Travassos, 1917c.

Echinorhynchus Zoega in Mueller, 1776, in part.

The concept of the genus *Echinopardalis* was first proposed by Travassos in 1917, under the unavailable, preoccupied name *Pardalis*. In the following year (1918) Travassos replaced the invalid name by rechristening the genus *Echinopardalis*, with *Echinorhynchus pardalis* Westrumb, 1821, the only assigned species, standing as the genotype. Meyer (1931a) added three presumptive species to this genus. All of the species reach maturity in the intestine of carnivores with cats and dogs serving as the most characteristic hosts. Up to the present time, records of members of this genus are restricted to South America and Egypt. In the present contribution *Echinopardalis macrurae* is recorded from a lynx, autopsied in the zoo at San Diego, California, as the first instance of occurrence of a member of this genus in North America.

Diagnosis of Echinopardalis.—With the characters of the family Oligacanthorhynchidae. Body relatively long. Proboscis armed with six spiral rows of six hooks each, many with large, asymmetrical roots extending both anteriorly and posteriorly from the base of the thorn. Lemnisci relatively long, cylindrical, reaching posteriorly at least as far as the testes. Reproductive organs of the male occupying about one-half the body length. Testes elongate ellipsoidal; eight cement glands in an elongated series immediately posterior to the testes. Eggs broadly elliptical, with concentric membranes of which the outer is not compacted.

Type of the genus: *Echinopardalis pardalis* (Westrumb, 1821).

***Echinopardalis macrurae* (Meyer, 1931a)**

(Plate 12, Figs. 109 to 113)

DIAGNOSIS.—With the characteristics of the genus *Echinopardalis*. Body relatively short, moderately heavy, tapering posteriorly. Females 11 to 43 mm long by 2.0 to 3.5 mm in maximum width near the anterior end. Males (according to Meyer, 1932) 20 mm long by 1.5 mm maximum width. Proboscis globular, about 0.35 to 0.45 mm long by 0.47 to 0.52 mm wide. Proboscis hooks in six spiral rows of six hooks each with beveled, chisel-like extremity to the tip of the thorn; some larger hooks with conspicuously asymmetrical anterior projection extending to the right, others with similar projection to the left; two basal hooks of each row with poorly developed root. Largest hooks, in anteriormost series, reaching an over-all length of 0.210 mm from tip of thorn to anterior extremity of root; succeeding three hooks diminishing in size with lengths ranging from 0.18 to 0.09 mm; the two hooks at base of each row variable in size, from 0.031 to 0.053 mm long. Lemnisci cylindrical, very long, in some females as much as 16 mm. Testes elongate, elliptical; eight cement glands arranged commonly in lateral pairs. Protonephridial excretory organs present. Eggs with mature acanthor ovoidal, with concentric membranes, 0.067 by 0.042 to 0.045 mm broad.

A series of five female specimens was obtained through the courtesy of Arthur L. Kelly. The host was a bobcat (*Lynx rufus*) unidentified as to variety, autopsied in the Biological Research Institute of the Zoological Society of San Diego, California, March, 1947. These individuals have been identified as *Echinopardalis macrurae* and this constitutes the first record of the occurrence of a member of this genus in North America. However, since the host was residing in a zoo, the source of the infection is wholly unknown and the parasite cannot be attributed with certainty to the endemic fauna of North America.

XV. ANALYSIS OF THE GENERA AND SPECIES OF THE FAMILY MONILIFORMIDAE EXAMINED IN THIS STUDY

As explained earlier in this monograph the family Moniliformidae includes but a single genus, Moniliformis. Historical treatment of this genus and its diagnosis will be followed by descriptions of the two species, *M. moniliformis* and *M. clarki* known to occur on this continent.

GENUS MONILIFORMIS Travassos, 1915b

Synonyms: *Echinorhynchus* Zoega in Mueller, 1776, in part.

Gigantorhynchus Hamann, 1892, in part.

Hormorhynchus Ward, 1917.

Moniliformis is the only genus ever ascribed to the family Moniliformidae. The genus knows no restrictions to continental boundaries and one of its species is potentially cosmopolitan in distribution. On several of the continents some distinctive species of limited geographical distribution have arisen. Many of the nominal species have been so inadequately described that extreme confusion still exists regarding the tally of species attributable to this genus. Some appreciation of the inadequacy of the specific descriptions is gained from the fact that after Meyer (1932) had reviewed the literature and weighed the evidences he gave three separate specific descriptions for *M. moniliformis*, quoting each from the publication of an earlier writer. If the three descriptions were based upon a single concept, as implied by application of a single name, Meyer made no attempt to adjudicate between those differences which might be ascribable to normal individual variability and those which reflect inaccurate or erroneous observation on the part of the original authors. In spite of this state of indecision regarding validity of the descriptions which presumably represent *M. moniliformis*, Meyer felt competent to set off as a new species (*M. dubius*) the material from rats of the United States. The descriptions of Moniliformis given by Chandler (1921) and by Van Cleave (1925) gave analytical details that had not been recorded previously for rats from other continents. Meyer took this as evidence that a distinct species is found in rats of North America. Later investigators have proved that the species of Moniliformis found in rats of other continents is identical with that found in North America. In consequence many investigators now regard *M. dubius* Meyer as a direct synonym of *M. moniliformis* (Bremser, 1811).

In 1925, Van Cleave reviewed the status of the genus Moniliformis in

North America. At that time he had before him an accumulation of collections received over a long period of years from colleagues in all parts of the world. A preliminary study of this extensive series of specimens led to the conclusion that two species exist on the North American continent. Specimens of one of these species seemed in every important respect directly comparable with forms from rats of other continents. These were therefore identified as *Moniliformis moniliformis*. The other species, which ultimately became known as *Moniliformis clarki* (Ward, 1917), had been reported from squirrels as the chief definitive host and this species seems to be confined to this continent. The early demonstration of this species and the uncritical references to the occurrence of *M. moniliformis* in squirrels by pioneer workers of the United States (e.g., Chapman, 1874) gave foundation to a belief that *M. clarki* might be the only species of the genus occurring in North America. The 1925 survey included specimens which Chandler had taken from rats in Texas and on which he (1921) had published observations without specific identification. These were readily recognizable as specifically distinct from *M. clarki*.

The information given by earlier workers seemed to indicate the presence of extreme variability in morphological features for the species which in other countries had gone under the name of *M. moniliformis*. On the basis of this assumption, supported by observations on the extensive series mentioned above, the specimens from Texas rats were identified as *M. moniliformis*. The agreement of these specimens with material from rats of other continents led to the assumption that *M. moniliformis* is a practically cosmopolitan species with a relatively high degree of individual variability. This pattern of geographical distribution seemed biologically sound since rats, as the definitive host, and cockroaches, as a larval host, have been transported from port to port around the globe by the vessels engaged in carrying merchandise and travellers.

In North America a single distinctive species limited to this continent (*M. clarki*) has been described up to the present time. Two additional nominal species have been recorded for North America. As a preview of details to be presented later in this chapter, the species attributed to this continent are *M. clarki* (Ward, 1917); *M. moniliformis* (Bremser, 1811), which since 1932 has commonly gone under the name *M. dubius* Meyer, 1932; and *M. spiradentatis* McLeod, 1933, which seems to be a direct synonym of *M. clarki*.

Diagnosis of Moniliformis.—With the characters of the family Moniliformidae. Body relatively large, elongate, usually with conspicuous pseudosegmentation involving only a portion of the trunk wall, since the body at each extremity is devoid of annulations. Proboscis cylindrical or club-shaped, with numerous distinctively crescentic, sharp-pointed hooks

which do not show clear distinction between thorn and root. Many of the roots notched or slightly bifid at the posterior extremity. Often a single small, flat, rounded sensory papilla is located on the external surface of the proboscis immediately posterior to the level of the basal hooks. Wall of proboscis receptacle composed of two diagonally arranged series of musculature which impress on it a distinctive spiral pattern. Retractors of the receptacle pass through its wall at the posterior extremity. Ganglion near base of receptacle. The lemnisci are long and narrow, each with a relatively small number of giant nuclei. Embryos with concentric membranes.

Mammals, especially rodents and their relatives, serve as definitive host; insects as intermediate hosts. In some species a fortuitous second intermediate host (amphibian or reptile) is found.

Type species of Moniliformis, by original designation, *M. moniliformis* (Bremser, 1811).

Family Relationship.—The acanthocephalan genus Moniliformis was named by Travassos in 1915, with *Echinorhynchus moniliformis* Bremser, 1811, the genotype, its only recognized species. For a short time prior to 1915, *E. moniliformis* had been very commonly assigned to the genus Gigantorhynchus. This generic assignment seems to have rested on the implicit belief by taxonomists of that day that large size is in itself a valid distinction for the genus Gigantorhynchus and for the family Gigantorhynchidae based upon it. Hamann, 1892, in his keen appreciation of fundamentals of morphology, had not mentioned *E. moniliformis* in listing the species attributable to the Gigantorhynchidae. Even of greater significance stands the fact that several morphological features cited for the family Gigantorhynchidae by Hamann would automatically exclude *Echinorhynchus moniliformis* from the genus Gigantorhynchus and at the same time would prevent the inclusion of the genus Moniliformis within the family Gigantorhynchidae. In spite of these inherent morphological contradictions, Travassos (1915b), assigned Moniliformis to the family Gigantorhynchidae, and there it remained until 1925 when Van Cleave called attention to the details which were regarded as basis for recognizing the Moniliformidae as a distinct family. Although the family Moniliformidae and genus Moniliformis have been very widely accepted in the literature, some textbook writers with extreme conservatism have ignored the morphological discrepancies and have continued down to the immediate present to use the name *Gigantorhynchus moniliformis* (see Brumpt, 1949:1038) for the species which occurs normally in rats and occasionally in man.

The name Hormorhynchus appears in the list of synonyms for Moniliformis given at the head of this section. Unaware of the fact that Moniliformis had previously been proposed as a generic name for this distinctive

concept, Ward (1917) proposed the name *Hormorhynchus* for the identical concept. Consequently that name becomes a direct synonym of *Moniliformis*.

Ordinal Assignment.—In a tabular comparison of the morphological features available for distinguishing the members of the four orders of Acanthocephala (Van Cleave, 1948) it has been pointed out that representatives of the genus *Moniliformis* deviate perceptibly from other genera that are assigned to the order Archiacanthocephala. This dissonance involves especially the structure of the proboscis receptacle. In all other members of the Archiacanthocephala there is a prominent cleft in the ventral wall of the proboscis receptacle through which the retractor and inverter muscles pass into the trunk cavity. In *Moniliformis* there is no such cleft because the receptacle is a closed muscular sac with the retractor and inverter muscles passing through small apertures in its posterior extremity. Furthermore, the structure of the receptacle wall of *Moniliformis* is entirely different from that found in other Archiacanthocephala. In other members of the order, the wall contains a single layer of transverse fibers while in *Moniliformis* there are two equally heavy layers of diagonally arranged muscle fibers. These are the only readily perceptible differences between *Moniliformis* and other genera of Archiacanthocephala. Inasmuch as there is consistent agreement in all other important morphological features, it has seemed best to regard the condition of the receptacle in *Moniliformis* as evidence of an independent line of evolution paralleling or approaching the condition found in the Palaeacanthocephala. It would seem wholly indefensible to recognize a separate order for *Moniliformis* on the basis of this one feature when other evidences point to consistent agreement between *Moniliformis* and other Archiacanthocephala. Ultimately it may be desirable to modify the diagnosis for the Archiacanthocephala so that the condition found in the proboscis receptacle of *Moniliformis* will not need to be cited as exceptional.

Species of the Genus Moniliformis in North America.—Van Cleave (1925) directed attention to the incompatibility of the descriptions of *M. moniliformis* appearing in the literature and expressed the opinion that the recorded differences were not objective features on which distinct species could be based. No single explanation is available for the discrepancies in either hook counts or simple microscopic measurements. Personal errors in observation and interpretation are in many instances the chief causes of recorded differences and closely related to these are the inconsistencies in accepted criteria. For instance, some investigators include the neck in measurements of the length of the proboscis. Inadequacy of sampling constitutes another basic difficulty encountered in comparing observations. It is well known that for some species of Acan-

thocephala the range of variability in such characters as the number of proboscis hooks is extremely small or even non-existent, as, for example, in the genus *Neoechinorhynchus*. In some other species, the number of hooks is subject to extreme individual variation. Except for certain instances of close phylogenetic relationship, it is impossible to predict ahead of time whether a given feature is going to show fidelity or variability within a given genus. In fact, two species of the same genus may be widely different in this respect.

Without adequate analysis, many of the earlier workers assumed a high degree of consistency in such measurements as hook length and size of eggs and followed the practice of citing but one or a very few measurements for each morphological feature. From the observations of Chandler (1947) and of others, it is now amply demonstrated that in material of *Moniliformis* from a restricted area and with identical host relations measurements of individual structures show much wider range than earlier writers had assumed to exist. Consequently, several species which have been regarded as distinct on the basis of minor differences from conditions mentioned in other descriptions must be reconsidered in the light of a broader basis of interpretation. Conversely, some of the material previously recognized as comprising a single highly variable species must be re-examined. Critical examination of a long series of specimens of any species of *Moniliformis* is almost certain to produce evidence that will extend the recorded range of individual variability in several respects. Too often, in the past, when differences have been observed in isolated samples these have been assumed to reflect evidence of taxonomic distinction and new species have been erected on insufficient grounds.

Machado Filho (1946) openly presented his objections to two of the Meyer names because he regarded both *M. dubius* and *M. travassosi* as direct synonyms of *M. moniliformis*. Through the collections of the Instituto Oswaldo Cruz, he had direct access to the material which Travassos had studied and could see no tenable distinction between *M. moniliformis* and the specimens which Meyer assumed to represent the species *M. travassosi*. The present writer concurs in that opinion.

***Moniliformis moniliformis* (Bremser, 1811)**

(Plate 12, Figs. 108A and 108B; Plate 13, Figs. 117 to 121)

Synonyms: *Echinorhynchus moniliformis* Bremser, 1811.

Gigantorhynchus moniliformis (Bremser, 1811).

Hormorhynchus moniliformis (Bremser, 1811) of Ward, 1917.

Moniliformis dubius Meyer, 1932.

Moniliformis travassosi Meyer, 1932.

DIAGNOSIS.—With the characters of the genus *Moniliformis*. Body exhibits considerable size difference for the two sexes; females may reach 320 mm, males 145 mm in length. Proboscis cylindrical to club-shaped.

0.50 to 0.64 mm in length by 0.15 to 0.24 mm in maximum width. Proboscis armed with distinctive crescentic hooks, not always in perfect rows, without sharp distinction between root and thorn; usually about 12 to 14 longitudinal rows of 10 or 11 hooks, occasionally 9 or 12 hooks, in each longitudinal series. Longest hooks 0.02 to 0.03 mm long, the measurement taken as a straight line from tip of thorn to back edge of the root. Lemnisci 4.0 to 7.5 mm long by 0.130 to 0.175 mm wide. Male organs confined to posterior non-annulated region of trunk. The testes very long, elliptical, in contact in young males but often widely separated in fully mature males. Eight cement glands pyriform in shape, commonly arranged in an elongated series but rarely as pairs. Embryos with fully formed concentric membranes from body cavity of mature female 0.090 to 0.125 mm long by 0.050 to 0.062 mm wide.

Definitive hosts: Rats seem to be the normal definitive hosts of *M. moniliformis* in North America but there is no record of the native cotton rat (*Sigmodon hispidus*) carrying an infection (Harkema and Karsten, 1949). The white laboratory rat has been infected experimentally. Moles of the genus *Scalopus* at times carry accidental infections.

There have been many surveys of rat parasites due to the interest in rats as carriers of the bubonic plague as well as to an interest in geographical distribution of helminths. In these surveys, rats of a given locality may be infected at one time and free from infection at another. There are positive records of *Moniliformis moniliformis* (or its synonym *M. dubius*) from the vicinity of Washington, D.C. (Price and Chitwood, 1931); Texas (Chandler, 1921); Maryland (Luttermoser, 1936); Mexico (Mazzotti, this paper); Cuba (Hoffman, 1938; Vigueras, 1936). In another survey at Washington, D.C. (Cram, 1928) no *Moniliformis* was found; and Caballero (1939) did not record *Moniliformis* from rats of Mexico City.

Due to the fact that there are no normal barriers to the establishment of *M. moniliformis* throughout this country, it is interesting to record regions where surveys have been wholly negative for *Moniliformis* in rats, as follows: New York (Herman, 1939); Quebec (Firlotte, 1948); Ohio (Forbes, 1942); Indiana (Cable and Headlee, 1937); Wisconsin (Moll, 1917). To this list may be added the results of surveys which have not been published with the following instances of negative records: Illinois (Van Cleave and students); Michigan (LaRue and students); Kansas (Ackert and students); Nebraska (Manter and students).

Intermediate host: the American cockroach (*Periplaneta americana*).

MATERIALS OF *Moniliformis moniliformis* FROM MAMMALS OF NORTH AMERICA EXAMINED IN THIS STUDY.*—

Host	Locality	Collector	Date	Accession number
<i>Rattus norvegicus</i>	Houston, Tex.	A. C. Chandler	1920	VC 1650
<i>Rattus rattus rattus</i>	Houston, Tex.	A. C. Chandler	1921	VC 1651
<i>Rattus norvegicus</i>	Houston, Tex.	A. C. Chandler	1920	VC 1652
<i>Rattus norvegicus</i>	Savannah, Ga.	S. Morris	Dec. 15, 1941	VC 3716
<i>Rattus</i> sp.	Mexico	L. Mazzotti	1949	VC 4403
<i>Scalopus aquaticus machrinus</i>	Urbana, Ohio	R. Rausch	June, 1944	VC 3775
<i>Scalopus aquaticus machrinus</i>	Urbana, Ohio	R. Rausch	June, 1944	VC 3776

***Moniliformis clarki* (Ward, 1917)**

(Plate 13, Figs. 122 to 129)

Synonyms: *Hormorhynchus clarki* Ward, 1917.*Echinorhynchus moniliformis* Bremser, 1811, in part.*Gigantorhynchus moniliformis* Bremser, 1811, in part.*Moniliformis spiradentatis* McLeod, 1933.

Ward (1917) named and described this species without pointing out any significant distinction, other than host relationship, between it and *M. moniliformis* of European investigators. Van Cleave (1925) gave the first morphological analysis which showed that *M. clarki* is a distinct species, clearly separable from *M. Moniliformis*. Chandler (1941) expressed the belief that *M. clarki* is a valid species and in 1947 gave a convincing summary of differences between *M. clarki* and *M. moniliformis* from rats, to which he applied the name *M. dubius*, proposed by Meyer.

DIAGNOSIS.—With the characters of the genus *Moniliformis*. Body large, in fully mature females reaching 400 mm in length. Proboscis cylindrical to clavate, relatively small, 0.28 to 0.42 mm long by 0.11 to 0.15 mm in maximum diameter. Proboscis hooks not arranged in perfect rows but in approximately 12 to 16 longitudinal series of 6 to 8 hooks each. Each hook crescentic in form, without sharp differentiation between thorn and root, a straight line measurement between tip of thorn and back edge of root 0.016 to 0.021 mm. Proboscis receptacle 0.67 to 0.84 mm long. Lemnisci 8 to 13 mm long by 0.07 to 0.10 mm in diameter. Embryos within fully gravid females, 0.06 to 0.09 mm long.

The writer has examined two small, isolated lots of *Moniliformis* which have given unusual difficulty in specific identification. One of these collections was taken by Dr. John S. Rankin, Jr. from a skunk (*Mephitis mephitis nigra*) at South Amherst, Massachusetts. All of these individuals were immature and some of the smaller ones seem to have a general ap-

* This list does not include numerous collections submitted for identification and returned to the collector before the writer began to keep a record of all material examined.

pearance different from that of *M. clarki*. However, an analysis of all the data showed that specifications overlap those for *M. clarki* and hence the original tentative identification as *M. clarki* is here retained. A second lot of specimens which Leidy collected from a "fox squirrel" likewise have minute proboscides but the specimens are so poorly preserved that accurate measurements are not available. Information on the label gives no indication as to locality from which these specimens were collected. In the absence of conclusive evidence to the contrary these specimens are also identified as *M. clarki*.

Definitive hosts: *Sciurus niger rufiventer* (western fox squirrel), *S. niger niger* (southern fox squirrel), *S. carolinensis* (eastern gray squirrel), *Glaucomys volans querceti* (Florida flying squirrel), *Citellus tridecemlineatus* (13-lined ground squirrel), *C. franklini* (Franklin's ground squirrel), *C. nelsoni* (Nelson's ground squirrel), *Scalopus aquaticus machrinus* (prairie mole), *S. aquaticus intermedius* (southern plains mole), *Tamias striatus fisheri* (eastern chipmunk), *Pitymys pinetorum scalopsoides* (mole pine mouse), *Geomys bursarius illinoensis* (Illinois pocket gopher), *Peromyscus maniculatus gracilis* (long-tailed deer mouse), *Eutamias* sp. (chipmunk), *Mephitis mephitis nigra* (eastern skunk).

Known geographical range in North America: north from Florida to New York, west through Ohio, Illinois, Michigan, Minnesota, Montana, Manitoba, Kansas, Oklahoma, and California. Chandler (1942) failed to find *M. clarki* in tree squirrels of southeastern Texas.

Intermediate hosts unknown.

MATERIALS OF *Moniliformis clarki* FROM MAMMALS OF NORTH AMERICA EXAMINED IN THIS STUDY.—

Host	Locality	Collector	Date	Accession number
<i>Sciurus niger rufiventer</i>	Kilbourne, Ill.	G. E. Clark	Feb. 27, 1909	VC 1756
<i>Sciurus niger rufiventer</i>	Kilbourne, Ill.	G. E. Clark	Feb. 27, 1909	VC 1757
<i>Sciurus niger rufiventer</i>	Illinois	H. E. Essex	Dec. 10, 1924	VC 2111
<i>Sciurus carolinensis carolinensis</i>	Murray Co., Okla.	H. Douthitt	Aug. 10, 1910	VC 1758
<i>Sciurus carolinensis carolinensis</i>	Idabel, Okla.	H. Douthitt	Sept. 1, 1910	VC 2229
<i>Citellus 13-lineatus</i>	Blair, Okla.	H. Douthitt	Apr. 5, 1910	VC 1757
<i>Citellus 13-lineatus</i>	Sulphur, Okla.	H. Douthitt	Aug. 14, 1912	VC 1760
<i>Scalopus aquaticus intermedius</i>	Kansas	J. E. Ackert	Oct. 21, 1922	VC 1762
<i>Scalopus aquaticus machrinus</i>	Grand Rapids, Mich.	C. W. Bazuin	Mar. 21, 1930	VC 2372

<i>Host</i>	<i>Locality</i>	<i>Collector</i>	<i>Date</i>	<i>Accession number</i>
<i>Scalopus aquaticus</i> <i>machrinus</i>	Ohio	J. R. Olive	Nov. 29, 1946	VC 3997
<i>Tamias striatus</i> <i>fisheri</i>	Cleveland, N. Y.	H. J. Van Cleave	Aug. 23, 1924	VC 2537
<i>Mephitis mephitis</i> <i>nigra</i>	N. Amherst, Mass.	J. S. Rankin	Nov. 11, 1936	VC 3042
<i>Peromyscus mani-</i> <i>culatus gracilis</i>	Pine Co., Minn.	A. B. Erickson	1937	VC 3326
<i>Citellus nelsoni</i>	San Benito Co., Cal.	A. C. Hawbecker	July 30, 1942	VC 3828
<i>Citellus nelsoni</i>	San Benito Co., Cal.	A. C. Hawbecker	Apr. 1, 1946	VC 3929
<i>Eutamias</i> sp.	Lincoln Co., Mont.	L. Adams	June 5-7, 1952	VC 4650
<i>Pitymys pinetorum</i> <i>scalopsoides</i>	Kingston, N. Y.	B. V. Travis	1952	VC 4615
<i>Geomys bursarius</i> <i>illinoensis</i>	Collinsville, Ill.	C. A. McLaughlin	Apr. 17, 1950	VC 4437

XVI. UNIDENTIFIABLE ARCHIACANTHOCEPHALA

At the close of the section on the Palaeacanthocephala, a list of materials of the genus *Corynosoma* that could not be identified to species was given. There is a similar, though smaller, lot of Archiacanthocephala in the collections studied by the writer to which neither generic nor specific names are applicable. Some of these are series of individuals which were taken from the preserved intestine of the mammalian host without preliminary treatment to ensure extrusion of the proboscis and many are immature individuals in which neither generic nor specific features are discernible. It would be folly to attempt to attach names to these wholly unsatisfactory specimens but the unnamed material will be listed by host and locality in the hope that some future worker may be fortunate enough to secure adequately prepared specimens for identification.

<i>Host</i>	<i>Locality</i>	<i>Collector</i>	<i>Accession number</i>
"Domestic cat"	Austin, Tex.	C. W. Deslandes	VC 4487
<i>Bassariscus</i>			
<i>astutus flavus</i>	Texas	H. L. Van Volkenberg	VC 3809
<i>Spilogale putorius</i>			
<i>putorius</i>	Grady Co., Ga.	R. Van Gelder	VC 4606
"Skunks"	U. of Cal.	VC 2164, VC 2165
"Coon"	Mendocino Co., Cal.	VC 2166, VC 2167

XVII. CHECK LIST OF THE SPECIES OF ACANTHOCEPHALA FROM MAMMALIAN HOSTS IN NORTH AMERICA

Throughout this monograph emphasis has been placed upon the fact that knowledge of the mammalian Acanthocephala of North America has unfolded very deliberately. Except for local lists, to the present time no North American investigator has ever compiled a list of the species from mammals of this continent. Even in those regions where intensive surveys have been conducted, as in Minnesota, through the investigations of Erickson (1938, 1946) the records of the occurrence of Acanthocephala in native mammals are surprisingly scarce. However, it should be explained that the Acanthocephala of mammals are not evenly distributed on this continent. There is a strong tendency for the Archiacanthocephala of mammals to be concentrated in the southern states where they have geographical continuity with the same or closely related species in the mammals of Central and South America. In like manner, the heaviest representation of Palaeacanthocephala in North American mammals is found in the Arctic and sub-Arctic regions where they have close taxonomic and biological relationships with the fauna of northern Europe. Thus most of the territory in the middle of the continent has a poorly developed acanthocephalan fauna depending upon the native mammals as definitive hosts. Under these circumstances, an intensive study of any restricted locality could never provide a fair sampling of the species distributed over the continent.

The earliest attempt toward the comprehensive listing of the species by hosts was that undertaken by Anton Meyer (1933) in his monograph of the Acanthocephala of the world. In that volume he prepared a section on host and geographical distribution, including all of the species mentioned in the literature. In that listing he did not treat Central and North America separately, but on the basis of the geographical distribution of the hosts it is clear that in 1933 only seven species of mammalian Acanthocephala had been recognized for the continent of North America. Taxonomically these species are arranged as follows:

Palaeacanthocephala : Polymorphidae

1. *Corynosoma strumosum* (Rudolphi, 1802)

Archiacanthocephala : Oligacanthorhynchidae (as here revised)

2. *Hamanniella tortuosa* (Leidy, 1850)
3. *Macracanthorhynchus hirudinaceus* (Pallas, 1781)

4. *Macracanthorhynchus ingens* (von Linstow, 1879)
5. *Oncicola canis* (Kaupp, 1909)

Archiacanthocephala : Moniliformidae

6. *Moniliformis dubius* Meyer, 1932 (= *M. moniliformis*)
7. *Moniliformis clarki* (Ward, 1917)

In the years intervening between 1933 and 1952 this list of species has been expanded until at the present time a total of twenty species are recognized as utilizing North American mammals as normal definitive hosts. Following the same taxonomic arrangement as that introduced above, these are:

Palaeacanthocephala : Polymorphidae

1. *Corynosoma strumosum* (Rudolphi, 1802)
2. *Corynosoma semerme* (Forssell, 1904)
3. *Corynosoma obtuscens* Lincicome, 1943
4. *Corynosoma reductum* (von Linstow, 1905)
5. *Corynosoma cameroni* Van Cleave, 1953
6. *Corynosoma hadweni* Van Cleave, 1953
7. *Corynosoma falcatum* Van Cleave, 1953
8. *Corynosoma validum* Van Cleave, 1953
9. *Corynosoma villosum* Van Cleave, 1953
10. *Bolbosoma balanae* (Gmelin, 1790)
11. *Bolbosoma vasculosum* (Rudolphi, 1819)

Archiacanthocephala : Oligacanthorhynchidae

12. *Macracanthorhynchus hirudinaceus* (Pallas, 1781)
13. *Macracanthorhynchus ingens* (von Linstow, 1879)
14. *Oncicola canis* (Kaupp, 1909)
15. *Pachysentis canicola* Meyer, 1931
16. *Echinopardalis macrourae* Meyer, 1931
17. *Hamanniella tortuosa* (Leidy, 1850)
18. *Hamanniella tumida* (Van Cleave, 1947)

Archiacanthocephala : Moniliformidae

19. *Moniliformis moniliformis* (Bremser, 1811)
20. *Moniliformis clarki* (Ward, 1917)

Seven of the foregoing species, known from North America only, have been named and described subsequent to 1933. The remaining additions to the Meyer list are species previously known from European or South American mammals which have extended their geographical range into adjacent parts of North America but these have only very recently been recognized in the fauna of this continent.

In the following section, the Acanthocephala known for each species of North American mammals are presented. In the literature it is unfortunate that many of the records cite only the common name of the host and

even in instances where the name of the species is given the name of the subspecies is often missing. From his information on geographical distribution of the subspecies, Dr. D. F. Hoffmeister has been able to furnish the writer with the names of many subspecies to make the records more exact. In many instances the original collector has verified the completed host names and has approved changes where invalid generic and specific names were corrected. It will be observed that many relatively large and important groups of mammals are omitted from the host list. In some instances this is due to the fact that food habits, as for example among the herbivores, are not conducive to acanthocephalan infection. On the other hand, there are many species and larger groups which may carry *Acanthocephala*, at least in part of their geographical range, but records have not yet found their way into the literature.

The general taxonomic arrangement of mammals developed by Simpson (1945) has been followed, with some simplification. Species regarded as accidental introductions into mammals are marked with an asterisk (*). In instances where juvenile or immature acanthocephalans are the only ones that have been encountered, that fact is recorded even though in many instances it is impossible to determine if the infection is normal or accidental.

Class MAMMALIA

Order Marsupialia

Family Didelphidae

Didelphis virginiana virginiana (common opossum)

Hamanniella tortuosa

Hamanniella tumida

Order Insectivora

Family Soricidae

Sorex palustris navigator (Rocky Mountain water shrew)

**Centrorhynchus* sp., juvenile

Family Talpidae

***Scalopus aquaticus* var.?** (common mole)

Macracanthorhynchus hirudinaceus

Scalopus aquaticus machrinus (prairie mole)

Moniliformis moniliformis

Moniliformis clarki

Scalopus aquaticus intermedius (southern plains mole)

Moniliformis clarki

Parascalops breweri (hairy-tailed mole)

Macracanthorhynchus ingens, immature

Scapanus townsendi (Oregon mole)

**Echinorhynchus* (?) sp., one cystacanth only

Order Edentata

Family Dasypodidae

Dasypus novemcinctus texanus (nine-banded armadillo)

Oncicola canis, juvenile cysts

Hamanniella tortuosa (?), immature

Order Rodentia

Family Sciuridae

Sciurus niger niger (southern fox squirrel)

Moniliformis moniliformis

Moniliformis clarki

Macracanthorhynchus hirudinaceus

Sciurus niger rufiventer (western fox squirrel)

Moniliformis clarki

Moniliformis sp.

Macracanthorhynchus hirudinaceus

Sciurus carolinensis carolinensis (southern gray squirrel)

Moniliformis clarki

Glaucomys volans querceti (Florida flying squirrel)

Moniliformis clarki

Tamias striatus fisheri (eastern chipmunk)

Moniliformis clarki

Macracanthorhynchus hirudinaceus

Eutamias sp. (chipmunk)

Moniliformis clarki

Eutamias minimus jacksoni (Lake Superior chipmunk)

Moniliformis sp.

Citellus tridecemlineatus (13-striped ground squirrel)

Moniliformis clarki

Citellus nelsoni (Nelson ground squirrel)

Moniliformis clarki

Family Geomyidae

Geomys bursarius illinoensis (Illinois pocket gopher)

Moniliformis clarki

Family Cricetidae

Peromyscus maniculatus gracilis (long-tailed deer mouse)

Moniliformis clarki

Neotoma sp. (wood rat)

Moniliformis sp.

Pitymys pinetorum scalopsoides (mole pine mouse)

Moniliformis clarki

Ondatra zibethica (muskrat)

**Polymorphus sp.*

Family Muridae

Rattus norvegicus (Norway rat)*Moniliformis moniliformis***Centrorhynchus spinosus*, experimental infection**Rattus rattus rattus** (black rat)*Moniliformis moniliformis***Rattus rattus alexandrinus** (roof rat)*Moniliformis moniliformis***Rattus sp.***Moniliformis moniliformis*

Order Cetacea

Family Monodontidae

Delphinapterus leucas (white whale)*Corynosoma cameroni**Corynosoma sp.***Mesoplodon bidens** (Sowerby whale)*Bolbosoma vasculosum*

Family Balaenopteridae

"Whale," unidentified as to sp. et gen.

Bolbosoma balanae

Order Carnivora

Family Canidae

Canis latrans (coyote)*Oncicola canis***Canis familiaris** (domestic dog)*Oncicola canis***Corynosoma semerme***Corynosoma strumosum***Urocyon cinereoargenteus** (gray fox)*Macracanthorhynchus ingens*, immature**Urocyon cinereoargenteus scotti** (Arizona gray fox)*Pachysentis canicola*

Family Procyonidae

Procyon lotor lotor (raccoon)*Macracanthorhynchus ingens***Centrorhynchus sp.*, juvenile**Neoechinorhynchus cylindratus*, immature**Echinorhynchus gadi*

Family Mustelidae

Mustela vison (mink)*Corynosoma strumosum***Corynosoma constrictum*

**Macracanthorhynchus hirudinaceus*

**Macracanthorhynchus ingens*, immature

Mustela erminea cicognanii (short-tailed weasel)

Moniliformis sp.

Mephitis mephitis nigra (eastern skunk)

Moniliformis clarki, immature

Macracanthorhynchus ingens, immature

***Mephitis mesomelas* var. ?** (skunk)

Pachysentis canicola

Spilogale leucoparia (spotted skunk)

Pachysentis canicola

Conepatus mesoleucas (hog-nosed skunk)

Pachysentis canicola

"Skunk," unidentified

Pachysentis canicola

Enhydra lutris (sea otter)

Corynosoma strumosum

Corynosoma villosum

Corynosoma sp.

Family Felidae

Felis domestica (domestic cat)

Oncicola canis

Lynx rufus (bobcat)

Oncicola canis

Echinopardalis macrourae

Suborder Pinnipedia

"Seal," unidentified

Corynosoma semerme

Corynosoma hadweni

Corynosoma villosum

Family Otariidae

Callorhinus alascanus (fur seal)

Corynosoma strumosum

Corynosoma semerme

Corynosoma villosum

Zalophus californianus (California sea lion)

Corynosoma strumosum

Corynosoma obtuscens

Eumetopias jubata (Steller's sea lion)

Corynosoma villosum

Corynosoma sp.

Family Odobenidae

Odobenus divergens (Pacific walrus)*Corynosoma validum*

Family Phocidae

Phoca sp., unidentified (seal)*Corynosoma strumosum**Corynosoma semerme**Corynosoma hadweni**Corynosoma validum***Phoca hispida** (ringed seal)*Corynosoma strumosum**Corynosoma semerme**Corynosoma reductum**Corynosoma hadweni**Corynosoma* sp.**Phoca vitulina** var.? (harbor seal)*Corynosoma strumosum***Phoca vitulina richardii** (Pacific harbor seal)*Corynosoma strumosum**Corynosoma* sp., unidentified**Halichoerus grypus** (gray seal)*Corynosoma strumosum**Corynosoma hadweni**Corynosoma falcatum***Erignathus barbatus** (bearded seal)*Corynosoma validum**Corynosoma hadweni*

Order Artiodactyla

Family Suidae

Sus scrofa domestica (domestic hog)*Macracanthorhynchus hirudinaceus*

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PLATES WITH EXPLANATIONS

PLATE 1

Corynosoma strumosum and *Corynosoma falcatum*

The scale accompanying Fig. 3 applies to all other drawings on this plate except those which have a separate scale accompanying the drawing.

FIGS. 1 through 15. *Corynosoma strumosum*, anatomical features.

1. Entire body of an immature female from the gray seal, *Halichoerus grypus*, of Alaska, in ventral view.

2. Proboscis of male from gray seal, *Halichoerus grypus*, of Alaska.

3. Praesoma and its attachment to the trunk in a female from the ringed seal, *Phoca hispida*, of Point Barrow, Alaska.

4. Praesoma and its attachment to the trunk in a male from the California sea lion, *Zalophus californianus*, from the collection of the Paris Museum.

5. Posterior extremity of a male with the copulatory bursa almost completely extruded, to show shape and arrangement of the genital spines. From the gray seal, *Halichoerus grypus*, Alaska.

6. Posterior extremity of a male with copulatory bursa fully introverted. From an unidentified seal of Alaska.

7. Posterior extremity of a very young male from gray seal, *Halichoerus grypus*, of Alaska.

8. Drawing of entire immature female from a mink, *Mustela vison*, taken at Corvallis, Oregon.

9. Praesoma and its attachment to the trunk in a male from the mink, taken at Corvallis, Oregon.

10. Posterior extremity of the trunk of a male from the mink, taken at Corvallis, Oregon, showing a very small portion of the copulatory bursa extruding from the genital pore. Compare especially with Fig. 5.

11. Entire body of an immature male removed from a visceral cyst of *Leptocottus armatus*, taken from Puget Sound, Washington.

12. Praesoma and its attachment to the trunk of the same individual as shown in Fig. 11. Compare with Fig. 2.

13. Posterior extremity of an immature male taken from a visceral cyst of *Leptocottus armatus* in Puget Sound, Washington.

14. Two mature embryos from the body cavity of a female from an undetermined species of seal, Alaska.

15. Two mature embryos from the body cavity of a female taken from the spotted seal of St. Lawrence Island, Alaska.

FIG. 16. Proboscis of a paratype female of *Corynosoma falcatum* showing distinctive form, size, and arrangement of the proboscis hooks.

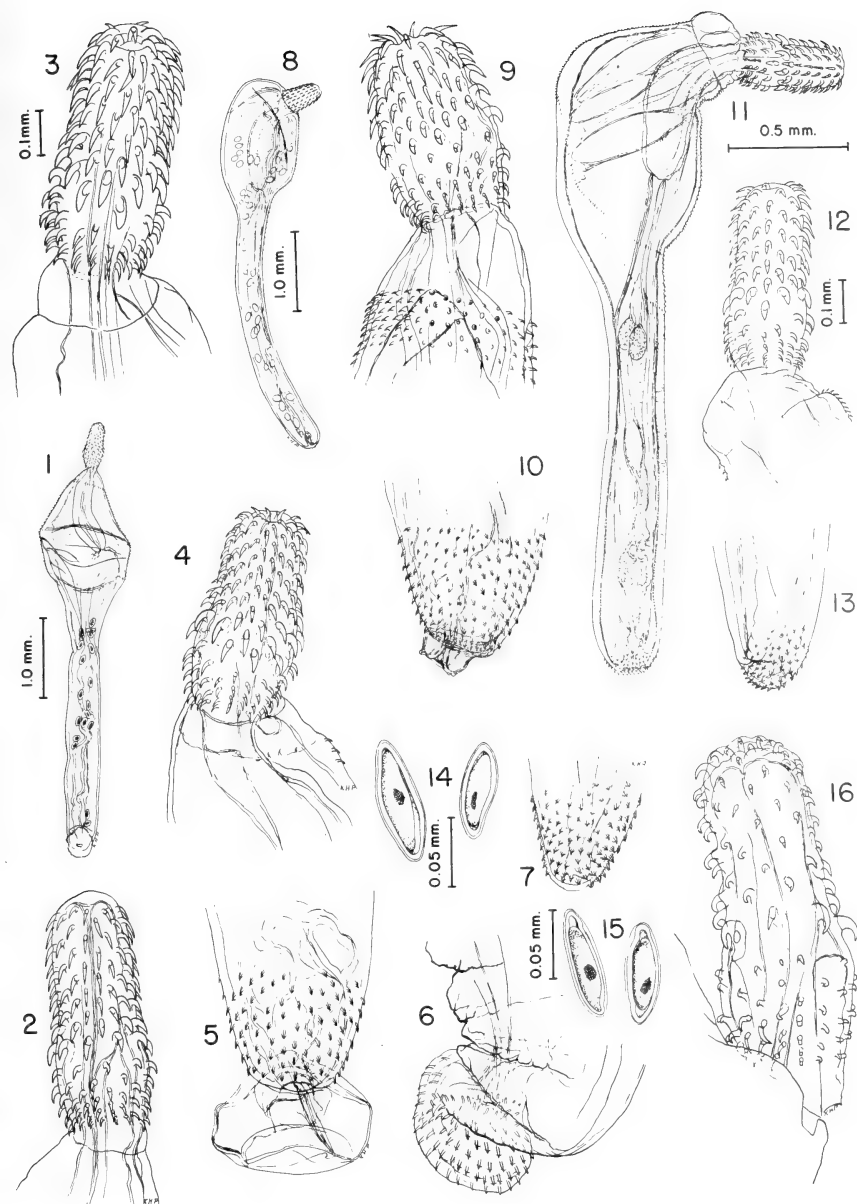


PLATE 2

Corynosoma semerme and *Corynosoma* sp. indet.

The scale beside Fig. 22 applies to all other drawings on this plate except those for which a separate scale is given.

FIGS. 17 through 28. Morphological details of *Corynosoma semerme*.

17 and 18. Simple outline to show size and form of body of characteristic females from the ringed seal, *Phoca hispida*, of Point Barrow, Alaska.

19, 20, and 21. General form and details of structure of specimens of *Corynosoma semerme* taken from *Phoca hispida* of Finland, identified by A. L. Forssell, author of the species. Fig. 19: Entire body of a mature female showing body form and some internal structures. Fig. 20: Praesoma and anterior region of trunk of female. Note that the neck is entirely retracted around the base of the proboscis and consequently not visible. Fig. 21: Posterior extremity of trunk of the same female individual as shown in Fig. 19, to show distinctive continuous distribution of trunk and genital spines without interruption along the ventral surface. Many of the spines ensheathed in a cuticular papilla.

22. Proboscis of immature male from the ringed seal, *Phoca hispida*, of Alaska. Spines of the fore-trunk omitted.

23. Praesoma of immature female from ringed seal, *Phoca hispida*, of Alaska. Spines of fore-trunk not shown.

24. Details of internal organization, drawn from a hemi-dissection of a male of *Corynosoma semerme* from intestine of a husky dog.

25. Details of body wall and genital tract of a female of *Corynosoma semerme*, as shown in a hemi-dissection of specimen from husky dog.

26. Details showing hook arrangement on proboscis dissected out of partially retracted female specimen from husky dog. Note that a portion of the base of the proboscis is missing.

27. Optical section of posterior extremity of ventral surface of trunk of gravid female of *Corynosoma semerme* from ringed seal, *Phoca hispida*, of Point Barrow, Alaska, showing shape and distribution of spines of hind-trunk and genital area.

28. Surface view of posterior extremity of trunk of a fully gravid female of *Corynosoma semerme* from ringed seal, *Phoca hispida*, of Point Barrow, Alaska, showing particularly the dispersal of the trunk spines.

FIG. 29. Proboscis of an unnamed species of *Corynosoma* from the sea otter, *Enhydra lutris*, of Alaska. Note that less than one-half of the proboscis is extroverted. The entire proboscis is distinctly longer than that of any known species of the genus found in the northern hemisphere.

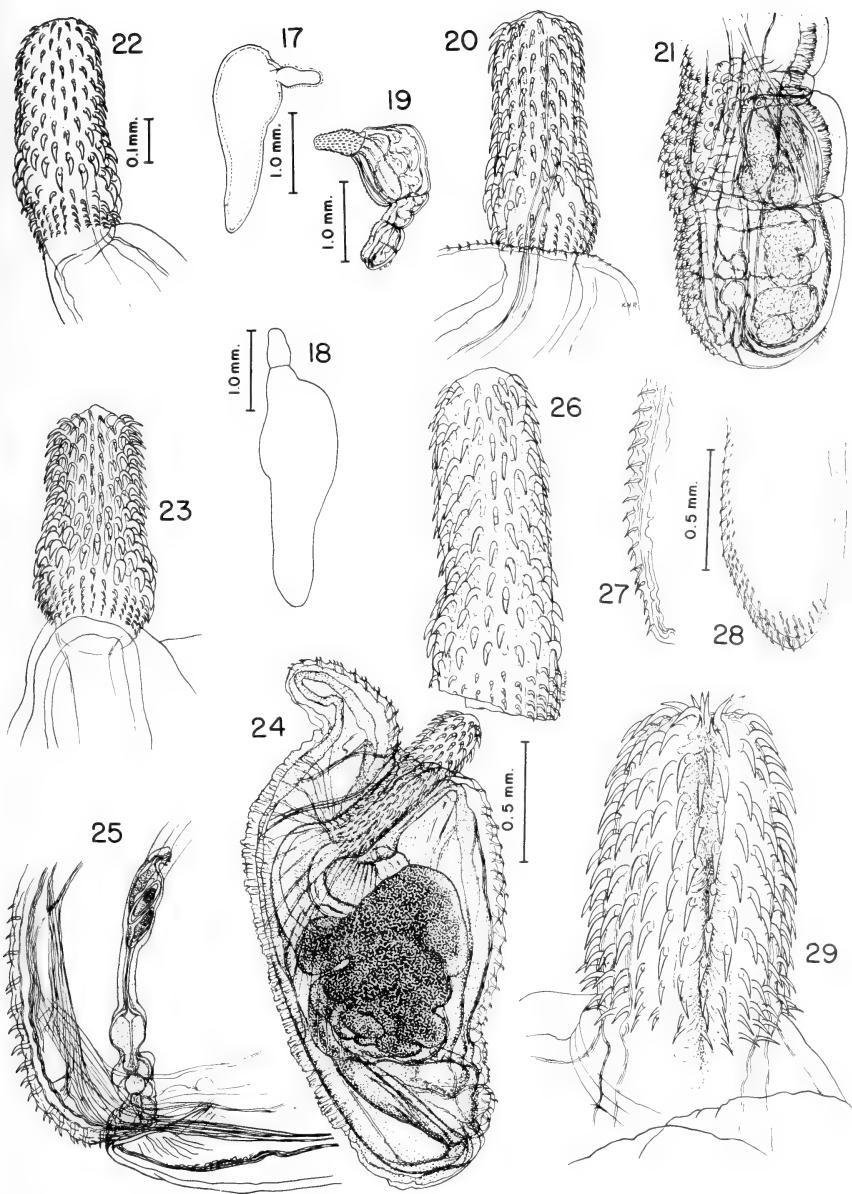


PLATE 3

Corynosoma cameroni and *Corynosoma obtusens*

All drawings to same magnification to which the scale accompanying Fig. 30 applies.

FIGS. 30 through 33. *Corynosoma cameroni* from white whale, *Delphinapterus leucas*, Lower Gulf of St. Lawrence, Quebec.

30. Proboscis of paratype male with its base and the neck retracted into the front end of the trunk.

31. Posterior extremity of a paratype male showing distribution of genital spines when the genital vestibule has just started to form.

32. Posterior extremity of the allotype male showing posterior extremity of the trunk partially introverted as a genital vestibule.

33. Posterior extremity of the holotype female showing genital vestibule completely introverted into the posterior extremity of the trunk, leaving no genital spines exposed on the surface of the body.

FIGS. 34 through 37. *Corynosoma obtusens* Lincicome, 1943, paratypes from the California sea lion, *Zalophus californianus*.

34. Praesoma and its attachment to the fore-trunk of a paratype female.

35. Optical section of posterior extremity of a paratype female showing a portion of the trunk wall bearing genital spines introverted as a genital vestibule.

36. Surface view of posterior extremity of a paratype male showing that the trunk spines of the male are not directly continuous with the enlarged genital spines.

37. Optical section of posterior extremity of a paratype female showing no break in distribution between genital and trunk spines, a few of the former already in slightly introverted vestibule.

FIGS. 38 and 39. Immature young of *Corynosoma obtusens* removed from visceral cysts of a marine fish, *Mycteroperca pardalis*, taken from near Mazatlán, Mexico.

38. External view of posterior extremity of immature female. Note that there is no interruption between trunk spination and the genital spines.

39. External view of posterior extremity of immature male showing an unspined region separating the spine field of the trunk from the area bearing genital spines.

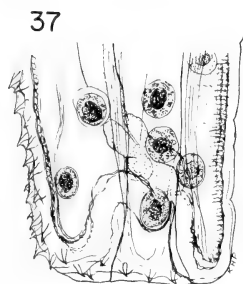
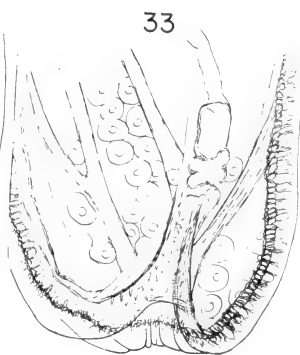
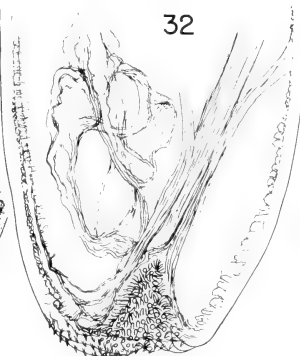
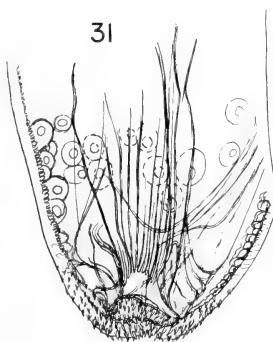
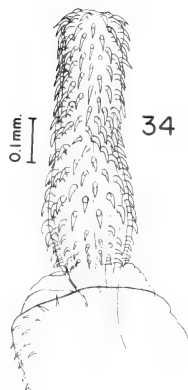
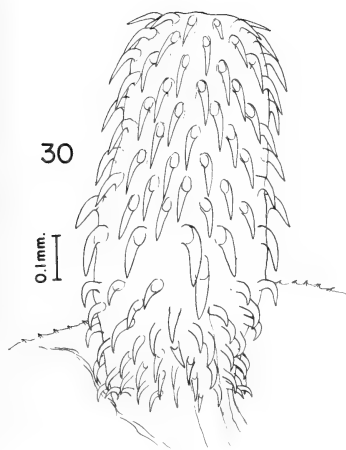


PLATE 4

Corynosoma validum

The scale accompanying Fig. 43 applies to all other drawings on this plate, except those which are accompanied by a separate scale.

FIGS. 40 through 42. Body shape and proportions of the two sexes.

40. Simple outline of a mature female from the spotted seal of Alaska, showing characteristic body shape of that sex, lacking an attenuated hind-trunk. Proboscis hooks and body spines omitted, because of low magnification.

41. Simple outline of a mature male from the Pacific walrus, *Odobenus divergens*, from St. Lawrence Island, Alaska. Note that the copulatory bursa is partially extruded at the end of the tapering hind-trunk. Proboscis hooks and body spines omitted.

42. An enlarged view of a paratype male from the Pacific walrus, *Odobenus divergens*, of Wainwright, Alaska. Arrangement of internal organs shown but proboscis hooks and trunk spines omitted.

FIGS. 43 through 46. Individual variations in the shape and proportions of the proboscis and its armature. All of this series drawn to same scale.

43. Praesoma and its attachment to the trunk in a paratype male from the Pacific walrus, *Odobenus divergens*, of Wainwright, Alaska. Neck partially retracted as shown by dotted line.

44. Praesoma of holotype female from the Pacific walrus, *Odobenus divergens*, taken at Wainwright, Alaska. Spines of fore-trunk omitted.

45. Proboscis of a paratype female from the bearded seal, *Erignathus barbatus*, of Point Barrow, Alaska.

46. Proboscis of a paratype female from the Pacific walrus, *Odobenus divergens*, of St. Lawrence Island, Alaska.

FIG. 47. Posterior extremity of a paratype male from the Pacific walrus, *Odobenus divergens*, taken at Wainwright, Alaska, showing arrangement, shape, and large size of the genital spines on the external surface of the hind-trunk.

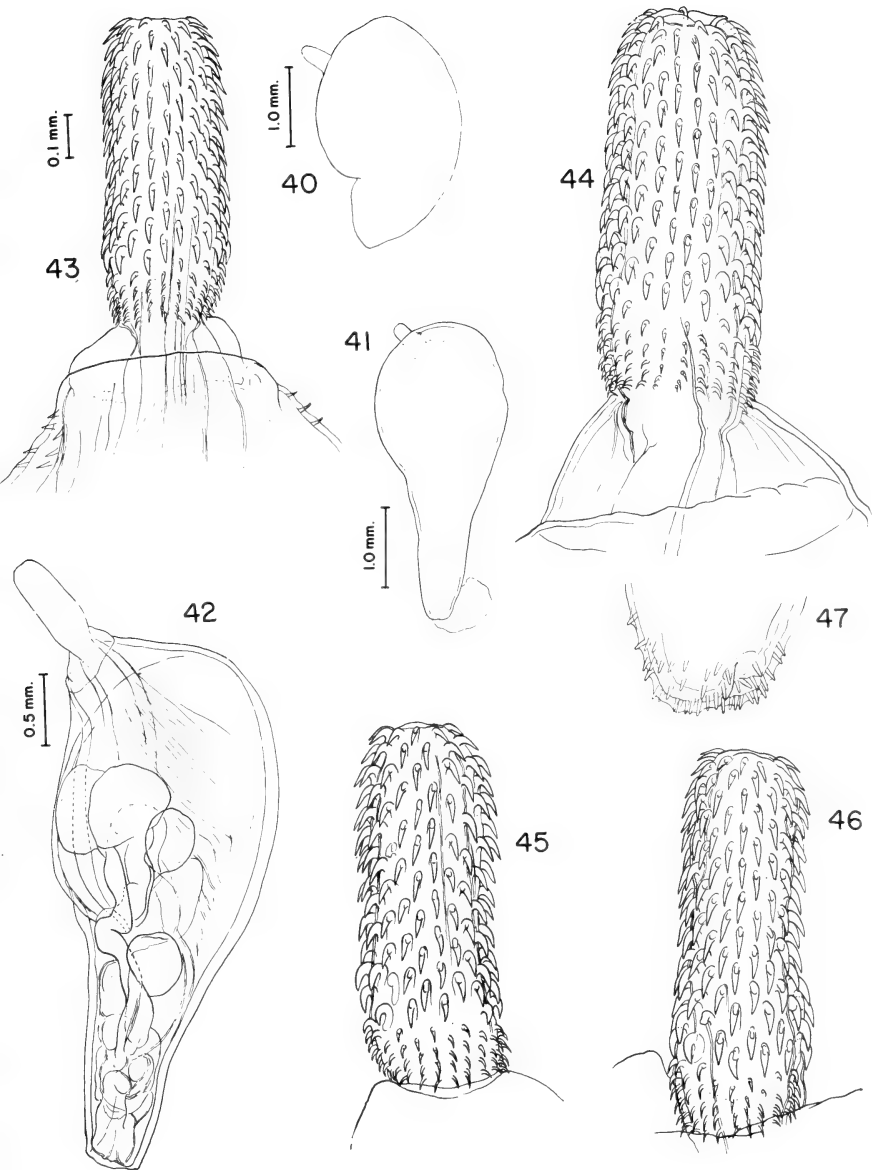


PLATE 5

Corynosoma reductum and *Corynosoma villosum*

The scale accompanying Fig. 48 applies to all drawings on this plate except the two for which a separate scale is shown.

FIGS. 48 through 50. Morphological details of *Corynosoma reductum* (von Linstow) taken from the ringed seal, *Phoca hispida*, in the vicinity of Point Barrow, Alaska.

48. Proboscis and portion of the neck of a female. Note that this is the largest proboscis shown for any species of *Corynosoma* found in the northern hemisphere. The number, shape, and diversification of the proboscis hooks are all distinctive of this species.

49. Posterior extremity of a male showing arrangement of size of the genital spines while on the surface of the trunk.

50. Posterior extremity of a male showing genital spines completely introverted within the genital vestibule.

FIGS. 51 through 57. Morphological details of *Corynosoma villosum* Van Cleave, 1953. All drawings from specimens taken from Steller's sea lion, *Eumetopias jubata*.

51. Organization and body shape of the holotype male taken on St. Lawrence Island, Alaska. See Fig. 57 for details of genital spines.

52. Proboscis of holotype male showing characteristic shape for the species.

53. Proboscis with disturbed hook arrangement.

54. Two mature embryos from a gravid paratype female.

55. Posterior extremity of a paratype female showing lip-like thinning of trunk wall adjacent to the vagina. No genital spines were present on this female.

56. Posterior extremity of a paratype female bearing genital spines in characteristic arrangement, size, and form.

57. Posterior extremity of holotype male (shown also in Fig. 51) showing arrangement and size of the large genital spines and the extruded copulatory bursa.

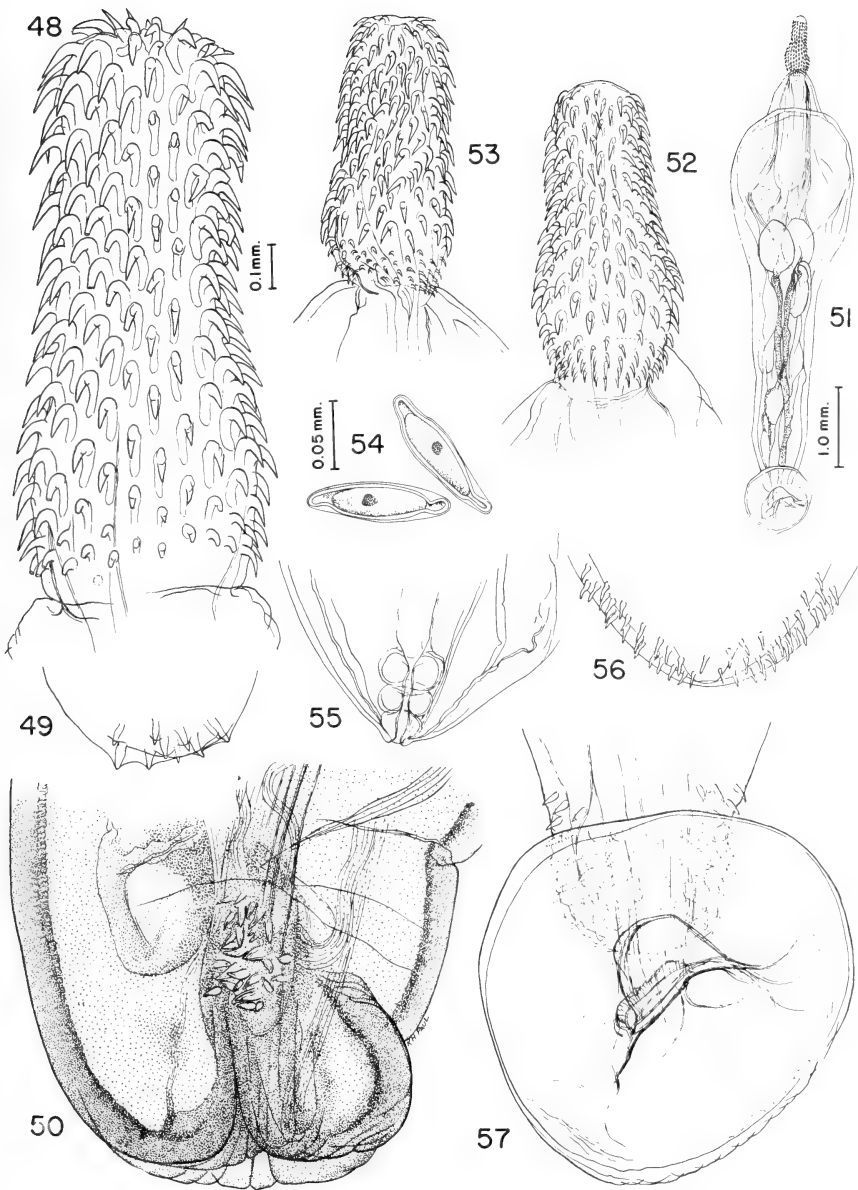


PLATE 6

Corynosoma hadweni

The scale accompanying Fig. 58 applies to all the outline drawings of entire individuals on this plate. An individual scale of magnification stands beside each of the other drawings.

FIGS. 58 through 60. Outlines showing body form and proportions of three characteristic paratype females; trunk spines and proboscis hooks omitted.

58. Fully gravid female from an unidentified seal of St. Lawrence Island, Alaska.

59. Mature female from a ringed seal, *Phoca hispida*, of Point Barrow, Alaska.

60. Mature female from a ringed seal, *Phoca hispida*, of Point Barrow, Alaska, showing shape of extended neck between proboscis and trunk.

FIG. 61. Proboscis of a female from ringed seal, *Phoca hispida*, partially retracted into front end of trunk without invagination. A portion of the trunk was dissected away to reveal the base of the proboscis.

FIG. 62. Three embryos from the body cavity of a gravid female from an undetermined species of *Phoca* collected at Kotzebue, Alaska.

FIG. 63. Three embryos from the body cavity of a gravid paratype female taken on St. Lawrence Island, Alaska.

FIGS. 64 through 66. Immature individuals of *Corynosoma hadweni* taken from visceral cysts of the smelt, *Osmerus mordax*, in Maine.

64. Outline drawing of entire immature individual to show body form.

65. Praesoma and its attachment to the fore-trunk. Note that the neck is fully extended between proboscis and trunk.

66. Proboscis of an immature individual with base and neck partially retracted into the front end of the trunk.

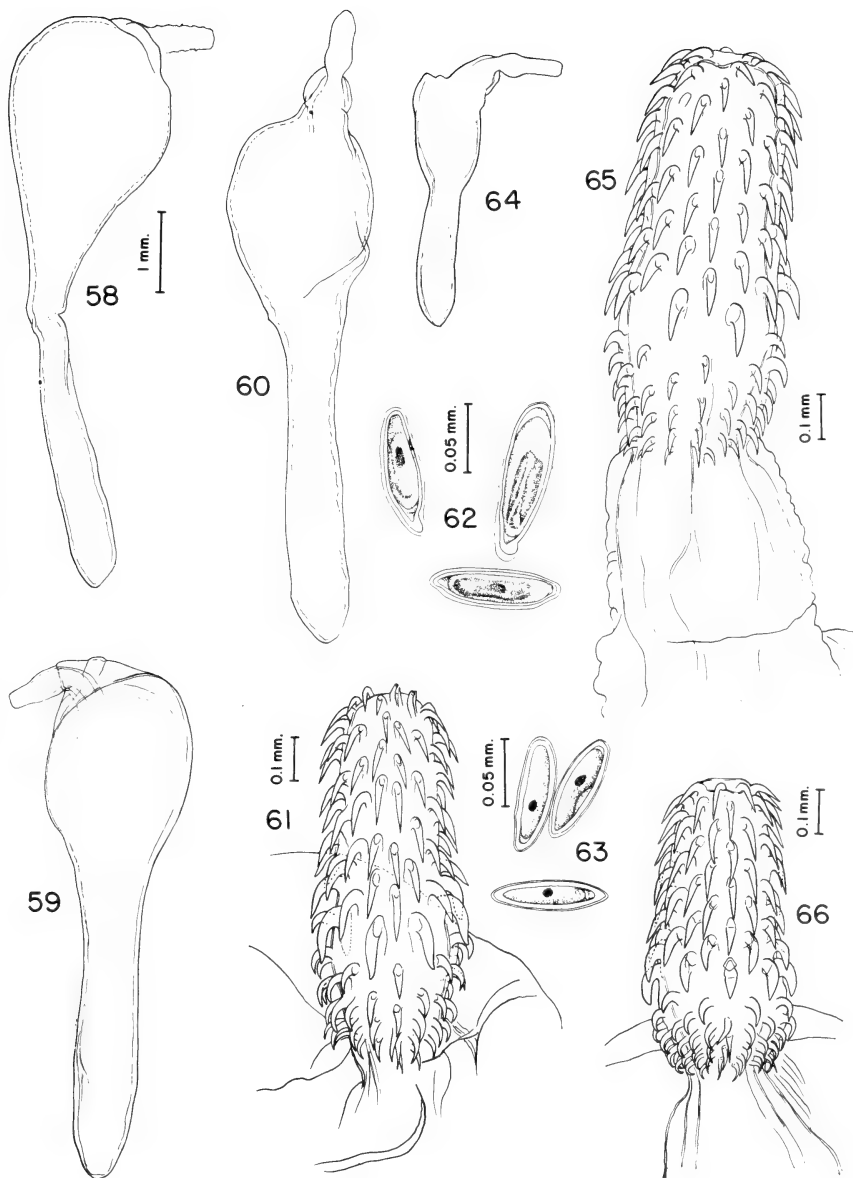


PLATE 7

Corynosoma hadweni

All drawings on this plate at the same magnification indicated by the scale accompanying Fig. 67.

FIGS. 67 through 72. Series of drawings showing individual variation in shape and size of the proboscis and in details of proboscis armature.

67. Proboscis of holotype female from the ringed seal, *Phoca hispida*, of Alaska.

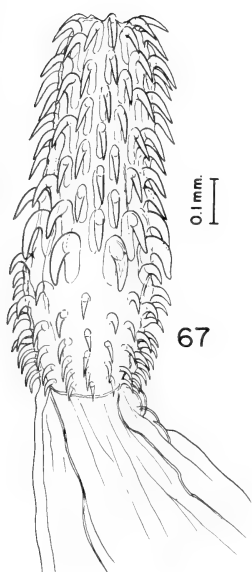
68. Proboscis of a paratype female from the gray seal, *Halichoerus grypus*, taken at Unalaska, Alaska.

69. Proboscis from an unidentified species of seal of Alaska.

70. Proboscis of a paratype female from an unidentified species of the genus *Phoca* taken at Kotzebue, Alaska. The proboscis of this individual represents about the maximum size for the species.

71. A long, narrow proboscis of a paratype female from an unidentified species of seal taken in Alaska.

72. Proboscis from a specimen taken from an unidentified species of seal in Alaska.



67



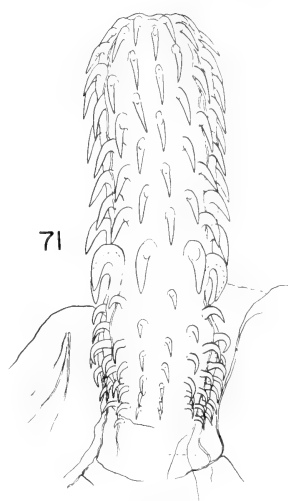
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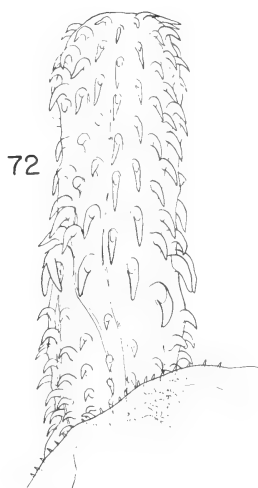
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PLATE 8

Bolbosoma

Figure 76 is drawn to the same magnification as indicated by the scales accompanying Figs. 74 and 75. There is a separate scale of magnification accompanying Fig. 73.

FIGS. 73 and 74. *Bolbosoma balanae* (Gmelin, 1790), from an unidentified species of whale taken at Seattle, Washington.

73. Outline drawing of praesoma and anterior portion of trunk.

74. Details of the proboscis and its armature.

FIGS. 75 and 76. *Bolbosoma vasculosum* (Rudolphi, 1819), from *Mesoplodon bidens*, locality in the United States unrecorded.

75. Praesoma and its attachment to the fore-trunk. Note especially the long unspined neck and the spination of the fore-trunk distributed in two mantles or spine fields.

76. Proboscis and a portion of the neck of another individual of *Bolbosoma vasculosum*, showing anterior tip of proboscis slightly invaginated.

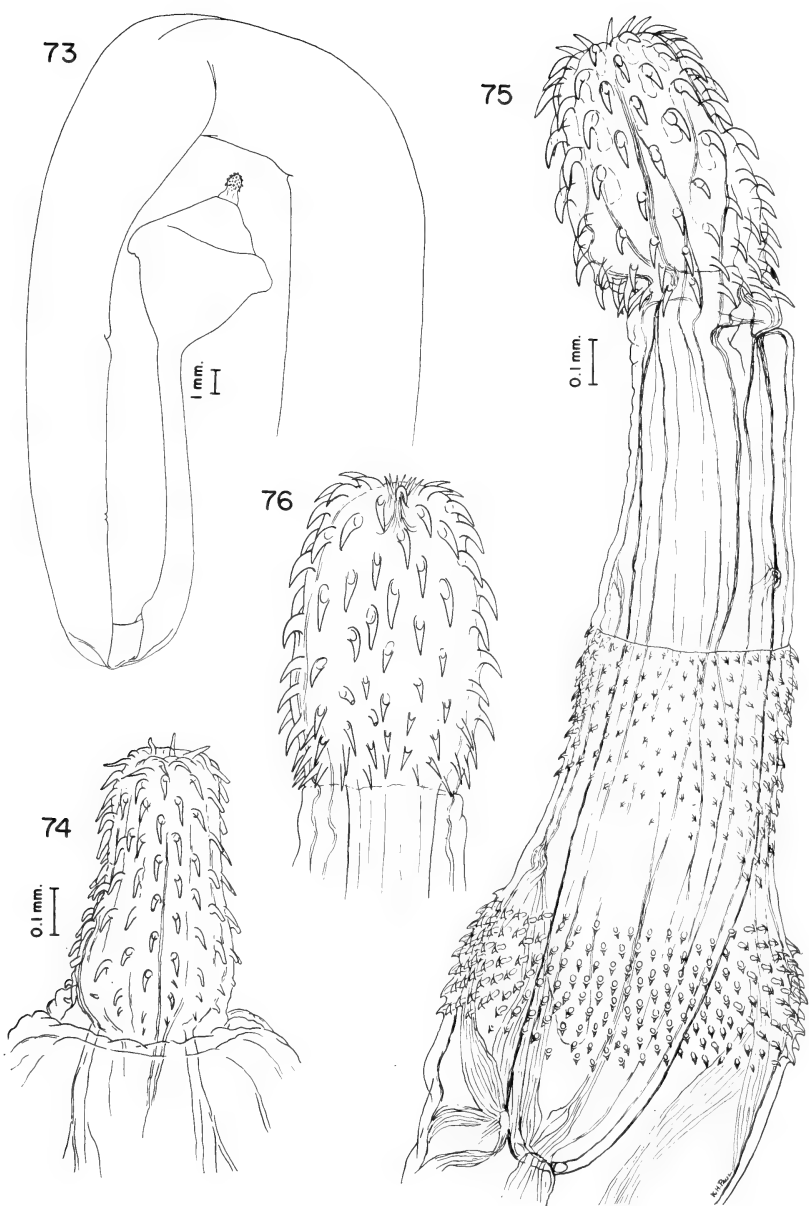


PLATE 9

Macracanthorhynchus

All drawings, except those for which a separate scale is provided, are at the same magnification as Fig. 84.

FIGS. 77 through 82. *Macracanthorhynchus hirudinaceus*, morphological details of taxonomic value.

77. External view of entire male and female with their proboscides implanted in a portion of the intestinal wall of a pig (After Van Cleave, 1947b.)

78. Details of a proboscis from the intestine of a pig, showing characteristic form and arrangement of hooks.

79 and 80. Proboscides from two individuals taken from the intestine of a fox squirrel, *Sciurus niger rufiventer*, of Radnor, Ohio.

81. Proboscis of an individual removed from the intestine of a pig.

82. Posterior extremity of a young male from intestine of a pig taken at Madison, Wisconsin. Note the cement glands (c) have not become fully differentiated but each is represented by one of the eight large elongated nuclei of a glandular rudiment.

FIGS. 83 and 84. *Macracanthorhynchus ingens* from the intestine of the raccoon, *Procyon lotor lotor*, of Texas.

83. Proboscis of a young male taken in Angelina County, Texas, showing characteristic number, form, size, and arrangement of the hooks.

84. Posterior extremity of trunk of a young female from which most of the subcuticula had been removed accidentally, showing the much branched protonephridial excretory organs (E) attached to the genital track anterior to the selective apparatus (s) of the uterus.

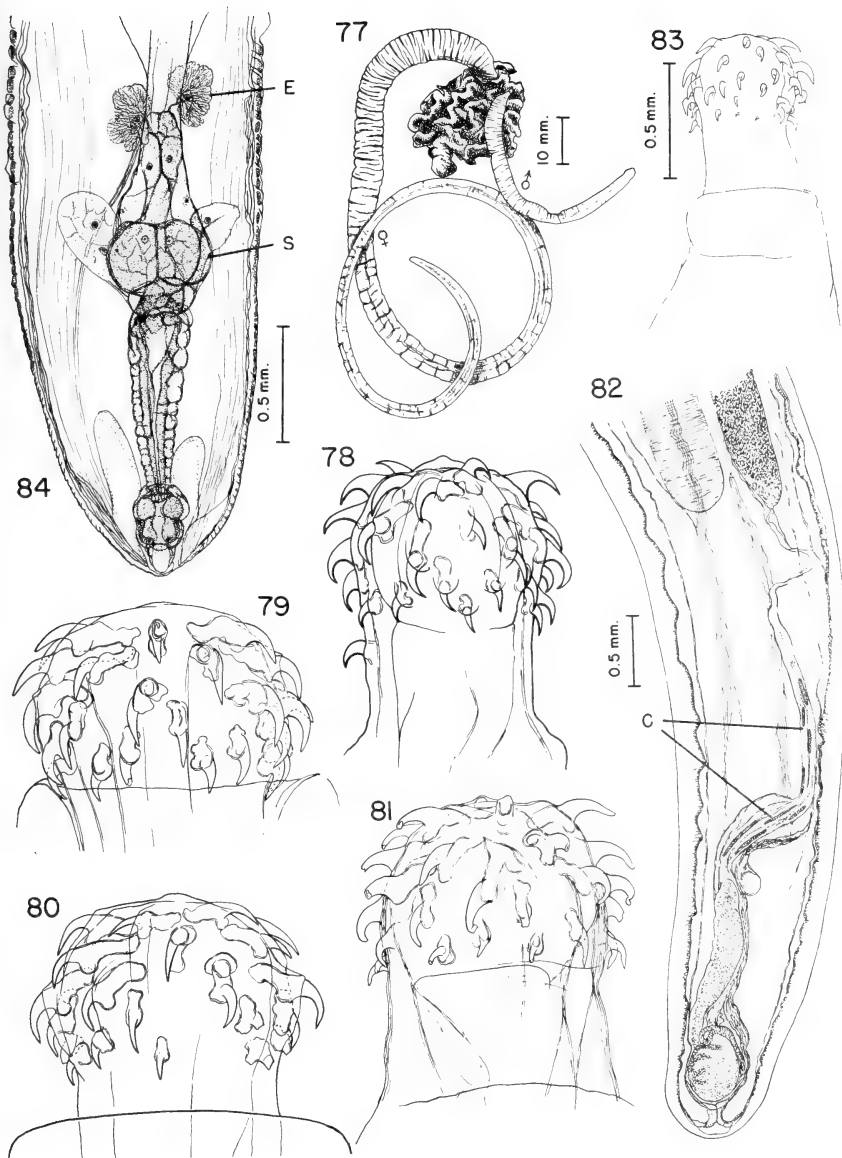


PLATE 10

Hamanniella and *Oncicola*

All the figures unaccompanied by a separate scale of magnification are at same magnification indicated by the line accompanying Fig. 88.

FIGS. 85 through 89. Morphological details of *Hamanniella tortuosa*.

85. Entire body of a mature female, surface view, showing characteristic size, shape, and surface markings. From an opossum, *Didelphis virginiana* taken at Idabel, Oklahoma.

86 through 89. Characteristic attachment organs from various localities, showing individual variation in appearance.

86. Praesoma and proboscis receptacle dissected from the preserved body of a contracted specimen from Louisiana. Note especially the cleft on the ventral wall of the receptacle, characteristic of the Archiacanthocephala.

87. Praesoma of a young male and its attachment to the trunk. From an opossum of Louisiana.

88. Proboscis of a mature male from South Miami, Florida.

89. Praesoma of a young male from Texas.

FIG. 90. Mature, embryonated eggs from the body cavity of a gravid female from South Miami, Florida.

FIGS. 91 through 95. Morphological features of *Hamanniella tumida* from *Didelphis virginiana*, near Fort Sill, Oklahoma. After Van Cleave, 1947a.

91. Outline drawing showing characteristic body form and relatively smooth surface of a young male.

92. Praesoma and anterior region of trunk of holotype female with most of the neck introverted within the trunk.

93. Praesoma of a paratype female.

94. Praesoma of a paratype female with proboscis slightly tilted to show apical view.

95. Genital extremity of a paratype female showing genital aperture (A), uterine bell (B), uterus (U), and vagina (V).

FIGS. 96 through 98. Distinctive features of the genus *Oncicola*.

96. Proboscis and anterior end of trunk of *Oncicola canis* from a coyote, *Canis latrans*, of Texas.

97. Embryos from the body cavity of a gravid female of *Oncicola canis*.

98. Proboscis of *Oncicola campanulata* from a leopard, courtesy of the Berlin Museum.

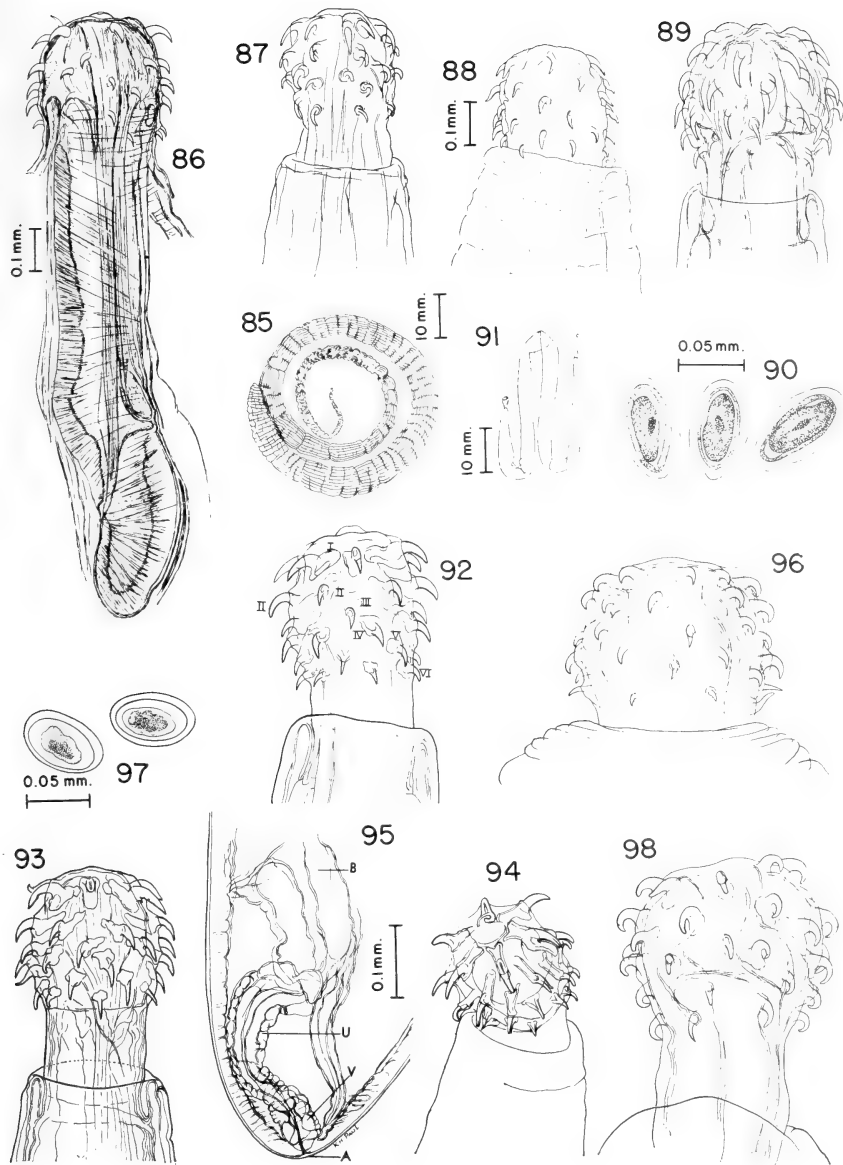


PLATE 11

Pachysentis canicola

The scale adjacent to Fig. 99 applies likewise to Figs. 100 and 101. The scale with Fig. 102 applies to all drawings of the proboscis and that beside Fig. 107 extends to the embryos only.

FIGS. 99 through 101. Outline drawings showing variations in shape and proportions of the body.

99. Mature male taken from the intestine of an unidentified skunk at College Station, Texas.

100. Mature female taken from the intestine of a gray fox, *Urocyon cinereoargenteus scotti* of central Texas.

101. Immature female from the intestine of a gray fox, central Texas.

FIGS. 102 through 106. Series of drawings showing range of individual variations in size, shape, and armature of the proboscis of *Pachysentis canicola*. Figs. 102 through 105, from a group of females from the intestine of a gray fox, *Urocyon cinereoargenteus scotti* of central Texas. Fig. 106, from intestine of an undetermined species of skunk of central Texas.

FIG. 107. Mature embryos from the body cavity of a gravid female taken from the intestine of a gray fox, *Urocyon cinereoargenteus scotti*.

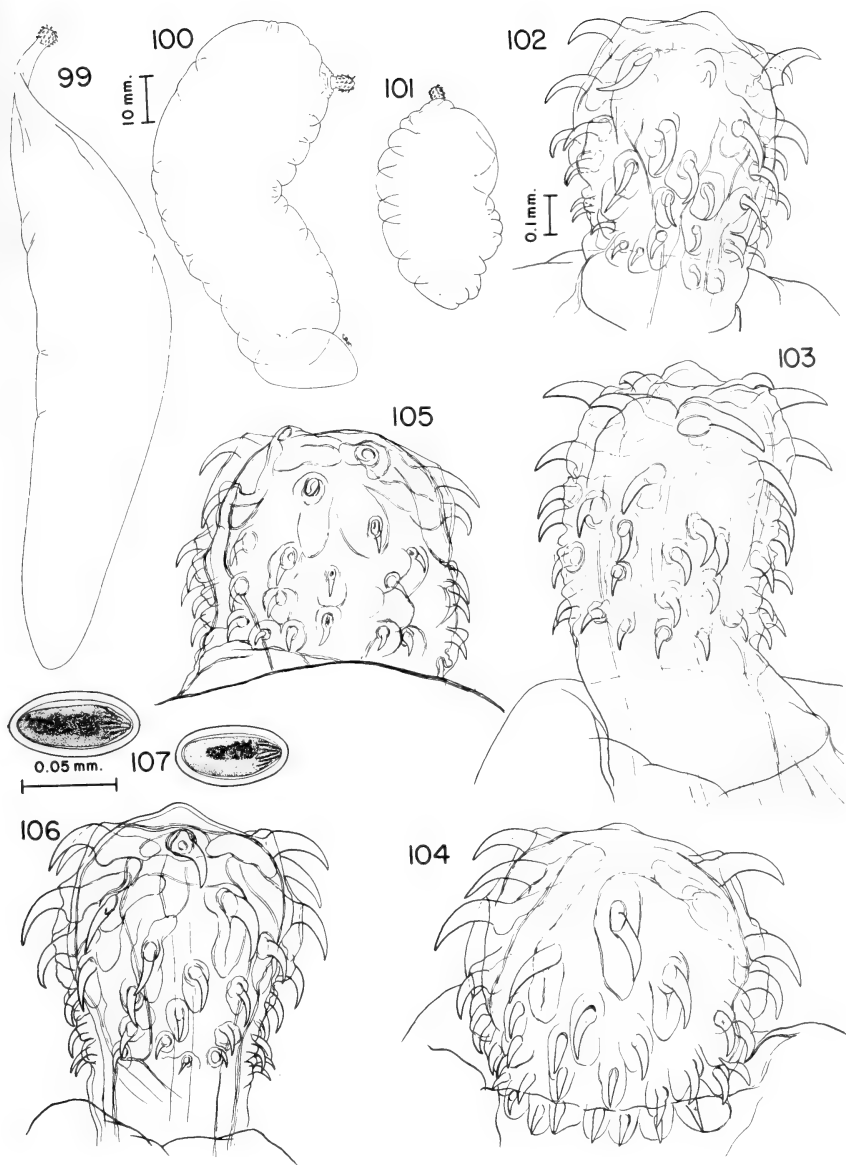


PLATE 12

Moniliformis, *Echinopardalis*, and *Pachysentis*

The scale accompanying Fig. 108A applies likewise to Figs. 110, 111, and 112; that with Fig. 114 applies also to Figs. 115 and 116. Magnification of each of the other drawings is indicated by an individual scale.

FIGS. 108A and 108B. Infective larvae of *Moniliformis moniliformis* from the intestine of a recently infected rat of Algiers, showing fully formed proboscis before body assumes definitive shape of the mature worm. Fig. 108B shows cystacanth still enclosed in the larval cyst.

FIGS. 109 through 113. Morphological details of *Echinopardalis macrourae* from *Lynx rufus* autopsied in the San Diego, California, Zoological Park. Origin of host unknown.

109. Simple outline showing general form of a mature female.

110. Proboscis and anterior portion of trunk of a gravid female showing distinctive form and arrangement of the proboscis hooks and their roots.

111 and 112. Proboscides from two different mature females.

113. Three mature embryos from the body of a gravid female.

FIGS. 114 through 116. Variations in the proboscis of different individuals of *Pachysentis canicola*, Figs. 114 and 115, from the intestine of an unidentified species of skunk; Fig. 116 from intestine of a gray fox. These three drawings are to identical scale but not as greatly magnified as those of the same species shown on Plate 11.

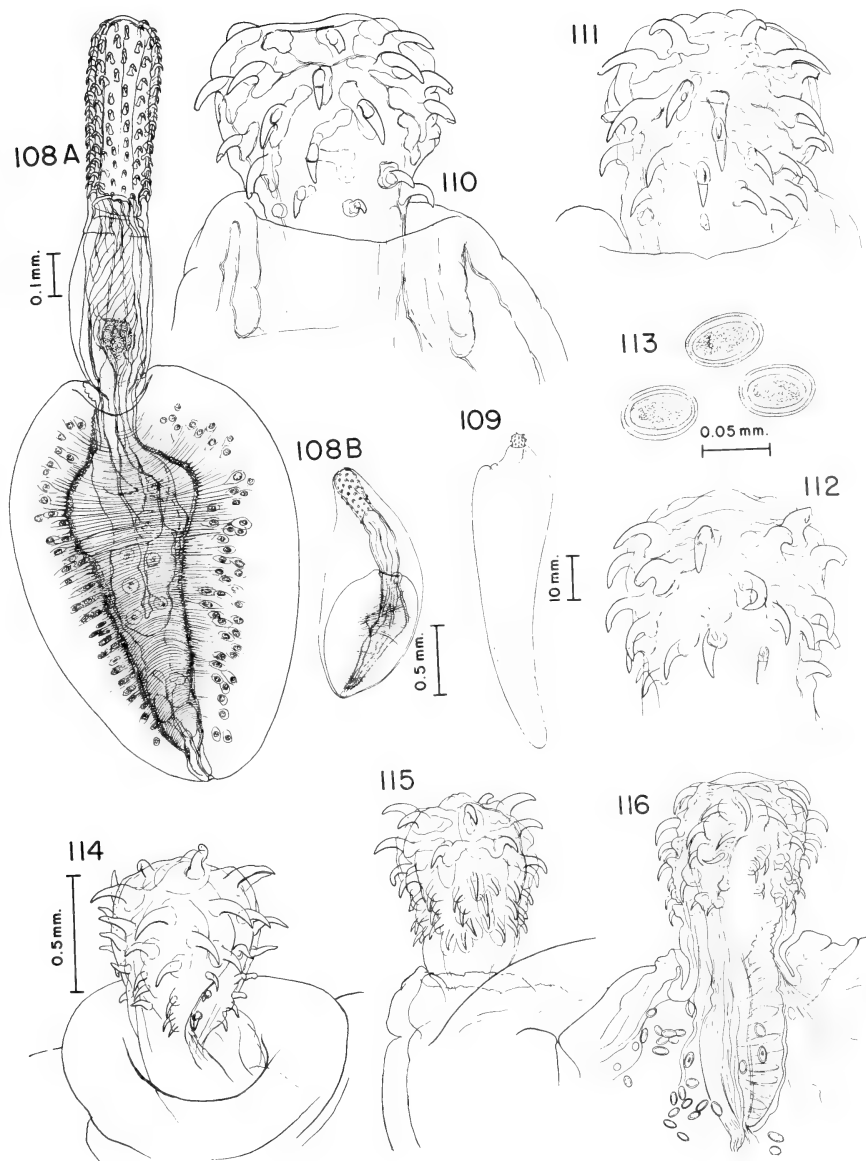


PLATE 13

Moniliformis moniliformis and *Moniliformis clarki*

All separate drawings of proboscides on this plate are at the same magnification as shown by the scale accompanying Figs. 117 and 129. The embryos shown in Figs. 120 and 130 are drawn to the scale indicated with Fig. 130.

FIGS. 117 through 121. Morphological details of *Moniliformis moniliformis* from North American mammals.

117 and 119. Proboscis and its attachment to the trunk in specimens from a rat at Houston, Texas. Note that in Fig. 117 the neck has been completely infolded around the base of the proboscis.

118. Proboscis and associated structures of a specimen taken from a mole, *Scalopus aquaticus machrinus*, of Urbana, Ohio, showing particularly the diagonal striation of the wall of the proboscis receptacle.

120. Eggs from a mature female from intestine of a rat, showing varied conditions of deformity of the outer membrane.

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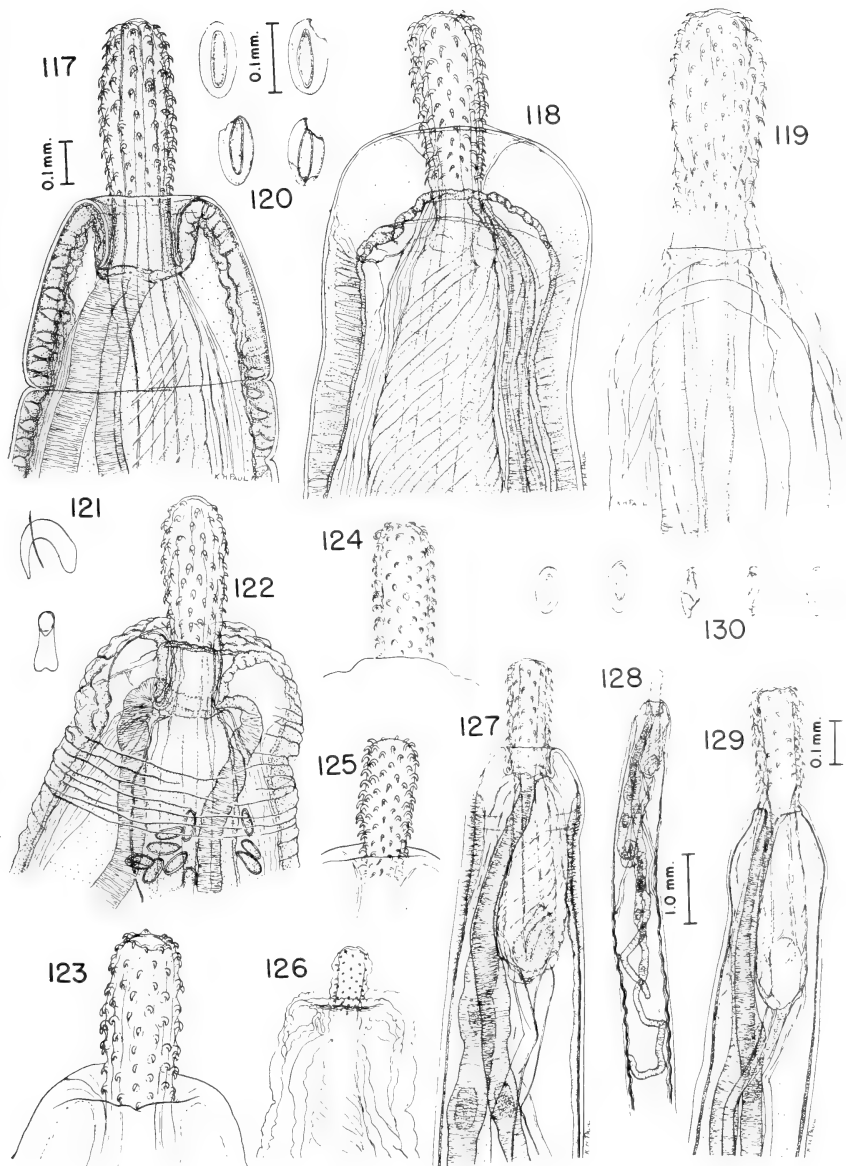
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The Evolution and Taxonomy of the Sarcophaginae (Diptera, Sarcophagidae)

SELWYN S. ROBACK

ILLINOIS BIOLOGICAL MONOGRAPHS: *Volume* XXIII, *Nos.* 3-4

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THE EVOLUTION AND TAXONOMY OF THE SARCOPHAGINAE

The Evolution and Taxonomy
of the Sarcophaginae
(Diptera, Sarcophagidae)

SELWYN S. ROBACK

ILLINOIS BIOLOGICAL MONOGRAPHS: *Volume* XXIII, *Nos.* 3-4

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I. Introduction

The calyptrate muscoid Diptera comprises one of the largest and most specialized groups of the Diptera or two-winged flies. The author (1951) proposed a classification of the calyptrate muscoids which divided them into three superfamilies: the Oestroidea, the Muscoidea, and the Sarcophagoidea. The Oestroidea includes the ox-warble flies, the heel fly, and a large group of insect parasites, the Larvaevoridae (Tachinidae). The Muscoidea includes the house fly, the latrine fly, the cabbage maggot, and their allies; and the Sarcophagoidea includes the Calliphoridae, or bluebottle-flies, and the Sarcophagidae, or flesh-flies. For further details and reasons for this classification, see Roback (1951).

The subfamily we are concerned with here, the Sarcophaginae, is one of two into which the Sarcophagidae is divided. The other is the Miltoigramminae. The species of this latter subfamily are generally small gray flies which, as far as is known, are parasitic in the nests of wasps and bees. The Sarcophaginae contains about 1,200 species which vary greatly in size and are generally gray in color, though gold pollinose and metallic colored forms are known. Their food habits vary from parasitism in humans to feeding in dung and decaying vegetable material. The male genital segments, especially in the genus *Sarcophaga*, are shiny red or black and protuberant.

Within the Sarcophaginae, the major problem has been the delineation of the genera. In the past various authors, such as Aldrich (1916), Enderlein (1928a), Townsend (1898-1938), Rohdendorf (1937), and Hardy (1943), have proposed classifications of the Sarcophaginae, or large parts of it. They have used a great variety of characters, external and genital, but no two authors have agreed fully on the supergeneric, generic, and subgeneric divisions to be used. Approximately 175 genera have been proposed within the Sarcophaginae by these authors. Their classifications, with the exception of Rohdendorf's (1937), while adding many names to the literature, have done little toward providing a sound basis for the generic classification of the Sarcophaginae.

It is the belief of the author that the best approach to a sound classification of any group is an understanding of its phylogeny. Only when the phylogeny has been determined can the relationships and natural divisions within the group be understood.

This work is an attempt to discover the probable phylogeny and the

genera and generic groupings within the Sarcophaginae, based primarily on aedeagal structure. A necessary corollary has been the determination of the homologies of the various sarcophagine aedeagal parts.

The general external anatomy of the Sarcophaginae shows very few characters that are of value in determining the paths of evolution of these flies, but the aedeagus, with its wealth of diverse structures, has been found to offer good morphological evidence upon which groupings and phylogenetic conclusions can be based.

Of necessity, this work can be of only a preliminary nature. The male aedeagus is only one facet of all the evidence which can shed light on this problem. The female genitalia must be studied, and more data will have to be gathered on the biology and immature stages. These are poorly known at present. Also many more species need to be studied and the parts of their aedeagi homologized with those described in this paper.

It is hoped that this study will contribute to a more sound and stable classification of the Sarcophaginae.

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MATERIALS AND METHODS

In the course of this study 145 species of Sarcophaginae were studied. Included in these 145 species are 70 per cent of the species listed by Aldrich (1916). Most of the material is Nearctic, but the Palearctic and Neotropical regions are represented. A few Australian species are included.

In addition to the species examined, 224 species were well enough illustrated and described to enable the author to place them definitely

in the genera treated here. Another 130 species were not as well illustrated or described, but could be tentatively placed within the genera. A very large residue of species either are described in literature not available to the author or could not even be tentatively placed on the basis of descriptions and figures available. The species seen, definitely and tentatively placed, are listed alphabetically after the generic or subgeneric descriptions.

The genitalia were studied by clearing them slightly in potassium hydroxide, washing in water, and then dissecting them in glycerine under the binocular microscope. In cases of very membranous phalli, uncleared specimens were also used. The drawings were made with the aid of a squared ocular grid.

The fifth sternite was dissected out and mounted in glycerine on a slide. These slides were projected with a small micro-projector and the drawings made directly on the projected image of the sternite.

II. Morphology and Terminology

Since the time of Pandellé (1896) and Böttcher (1912-13), the genitalia of the sarcophagids have been used as the major criterion for differentiating and grouping the species. As can be seen in Chart 1, most investigators have worked chiefly within the *Sarcophaga* group. The great variety of phallic structures within this and the other groups of the Sarcophaginae have not been homologized. This discussion is an attempt to describe and elucidate the probable lines of evolution and homology of the parts of the aedeagus within the Sarcophaginae.

With regard to the possible function of all the complex structures found in the phallus, little can be said. I have examined the interlocked genitalia of several species and must, for the present, agree with Patton (1939) that there is nothing in the female genitalia to explain or necessitate such a complex phallus in the male.

ABDOMEN

The abdomen of the Sarcophaginae is divided into two sections, the preabdomen and the postabdomen.

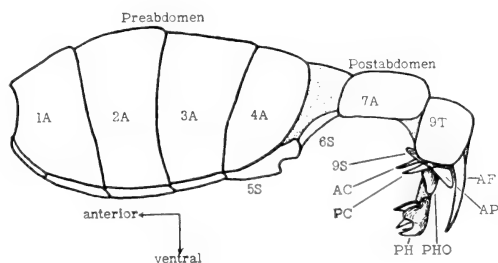
The preabdomen consists of morphological segments one to five. The first and second segments are fused and considered as the first abdominal in most taxonomic papers. The second, third, and fourth abdominal segments in most taxonomic papers are the third, fourth, and fifth morphological segments. In order to avoid confusion the terminology of these taxonomic systems has been retained in the classification section of this work. Each of the segments consists of a ventrally prolonged tergite and a small sternite placed in the membrane between the ventral edges of the tergite. The fifth sternite is often highly modified and closely associated with the postabdominal segments.

The segments posterior to the morphological fifth, six to nine, constitute the postabdomen. These are highly modified and bear the aedeagus and its associated structures. The sixth sternite is reduced to a latero-ventral band associated with the fifth sternite. The sixth tergite has been lost. The fused seventh and eighth abdominal segments and the ninth segment are generally well sclerotized and form a capsule to protect the aedeagus at rest. They generally fold into the fifth segment forming a cap-like structure at the tip of the abdomen, Fig. 460. They may be large and protuberant as in Fig. 460, or small and hidden by the fifth

morphological tergite. In the Agriini the fused seventh and eighth segments are connected to the fifth by a short membrane, while in the Sarcophagini the membrane is very long, permitting the postabdominal segments to be greatly separated from the preabdomen. The fused seventh and eighth segments will be referred to simply as the seventh abdominal segment. Morphologically they are the sternites of their segments, the tergites having been lost.

The paired anal forceps (AF), Figs. 5 and 334, are placed caudo-ventrally in relation to the ninth tergite. On each side at the ventro-caudal edges of the ninth sternite are the anal plates (AP). The ninth sternite is located between the ventral edges of the ninth tergite. On each side of the ninth sternite, anterior to the anal plates are the anterior and posterior claspers. Projecting ventrally from the center of the ninth sternite, when the postabdomen is extended, is the aedeagus. At rest it is horizontal within the abdomen.

The relationship and orientation of the structures discussed above are shown in Text Fig. 1. The figures on the plates are oriented in a like manner.



TEXT FIGURE 1. Diagrammatic lateral view of sarcophagine abdomen.

THE FIFTH STERNITE (5S)

The fifth sternite is the indented, last visible sternite. It usually consists of a basal section and two divergent arms and is either V- or Y-shaped depending on the length of the basal section. The parts of the sternite as used in this work will be the sternal base (B), the sternal arms (A), and the sternal window (W). This last is formed between the bottom tip of the V in the fifth sternite and the cross attachment of the sixth sternite. In the fifth sternite, in which there is no window, the sixth sternite is attached below the lower apex of the V.

The other external features of the Sarcophaginae have been well described and treated in the literature, and there is no need for any extended discussion of them here. While showing some tendencies, they were of little value in working out the phylogeny of the subfamily.

AEDEAGUS

On the basis of a consideration of all the aedeagal parts found within the Sarcophaginae, the following ancestral aedeagus can be postulated, Fig. 1:

- I. Phallophore—A simple, sclerotized, short tube, dorsally articulating with the ninth sternum and ventrally bearing the phallus.
- II. Phallus—Attached to phallophore by membrane, consisting of the following parts:
 - a) Corpus—tubular basal piece of phallus; longitudinally divided into membranous and sclerous portions.
 - b) Phallic tube—an antero-ventral constriction of the membranous area of the corpus.
 - c) Ventral sclerotization—a transverse, ventrally divided sclerotized band present in the membranocorpus below the phallic tube.

The structures present in the above hypothetical aedeagus have given rise, along different lines, to all the aedeagal structures of extant Sarcophaginae.

Among present-day muscoids, the aedeagi of the Scopeumatinae and in particular those of *Scopeuma stercorarium* (Linn.), Figs. 3 and 4, and *Spathiophora cincta* Loew., Figs. 7 and 8, closely approximate the hypothetical aedeagus.

PHALLOPHORE (PHO)

This is the tubular, sclerotized basal portion of the aedeagus. As previously mentioned, it articulates dorsally with the ninth sternum; ventrally it bears the phallus. It is present in all Sarcophaginae, generally connected to the phallus by a membrane, but connate with it in *Ravinia*, *Oxysarcodexia* and *Cistudinomyia*, Figs. 246 and 280. A few of its variations are shown in Figs. 25, 58, 309, 316. It never bears any appendages.

PHALLUS (PH)

This is the apical section of the aedeagus. Basically it consists of a partly sclerotized, partly membranous tube (called the *corpus*), Fig. 1, the phallic tube and the ventral sclerotization. In the more specialized sarcophagids it develops into a very complex structure with many appendages arising from the corpus and internal parts. Instead of discussing it as a whole, which is rather impractical, we shall consider each one of its parts and its development separately. Chart 2 shows the development of the parts in graphic form, and Chart 3 shows the development of the ventral sclerotization.

CORPUS (C)

As the name implies, this is the body or basal section of the phallus. In its most generalized form, Fig. 1, it could be described as a short tube longitudinally divided into sclerous and membranous portions. These are the sclerocorpus and membranocorpus, respectively. In most cases, the membranocorpus is reduced or non-existent, and the resultant structure will simply be called and labeled the corpus. Only in *Camptops unicolor* Ald. and *Chloronesia* sp., Figs. 36 and 41, is there a well-defined membranocorpus.

Seen in profile, the sclerocorpus extends forward dorsally, while ventrally the membranocorpus constricts to form the phallic tube and then curves inward and downward with the ventral sclerotization.

From this hypothetical corpus, the semi-tubular corpus of the subtribe Servaisiina, such as in Figs. 362, 378, 386, and 393, can easily be derived by the reduction of the membranocorpus and the slight extension and modification of the sclerocorpus.

In some cases, such as *Rafaelia rufiventris* Tns., Figs. 310 and 311, *Euboettcheria australis* Tns., Figs. 305 and 307, and *Sarcodexia lambens* (Wied.), Fig. 302, the dorsal extensions of the sclerocorpus have formed a complete closed ring. This is not the usual case in the Sarcophaginae.

In the Raviniina and *Wohlfahrtia vigil* (Walk.), Figs. 18, 19, and 220-286, the corpus has closed over ventrally and elongated, thus forming the characteristically shaped corpus of both. Parker (1914), on the basis of this development, believed that *Ravinia* and *Wohlfahrtia* were related, but the development is apparently quite independent in each case.

All the variations of form of the corpus can be derived from the hypothetical type, Fig. 1, by variation in the size and shape of the sclerocorpus. They are too numerous to be taken up individually.

In the Sarcophagini, the corpus has given rise to the vesica, juxta, lateral plates, harpes, dorsal rods, and explanate vesica (see Chart 2).

PHALLIC TUBE (PT)

The phallic tube is an antero-ventral prolongation of the membranocorpus. It is present in all the Agriini seen, being large in *Agria affinis* (Fall.), Figs. 12 and 13, and *Sarcofahrtia ravinia* Park., Figs. 14 and 15, and reduced in *Wohlfahrtia vigil* (Walk.), Figs. 18 and 19. In some of the Sarcophagini it is clearly present though much reduced. This can be seen in *Johnsonia* (*Emblemasoma*) *erro* (Ald.), Fig. 46, and *Johnsonia* (*Johnsonia*) *rufitibia* (Wulp), Figs. 48 and 49. In a few other Sarcophagini, such as *Paraphrissopoda amoena* (Ald.), *P. capitata* (Ald.), *P. hillifera* (Ald.), and *Camptops unicolor* Ald., Figs. 294, 297, 299, and

36, it is apparently represented only by a vestigial sclerotization. *Imparia impar* (Ald.), Figs. 20-22, possesses what is apparently a highly developed phallic tube. It is completely absent in all other Sarcophagini.

LATERAL PLATES (LP)

These are plate-like lateral sclerotizations, apparently developed from the membranous section of the corpus. They are clearly present in *Johnsonia* (*Emblemasoma*) *erro* (Ald.), Fig. 46, *Johnsonia* (*Johnsonia*) *rufitibia* (Wulp), Fig. 48, *Johnsonia* sp., Fig. 44, and most of the members of the genus *Helicobia*. *Kellymyia kellyi* (Ald.), Fig. 309, and the members of *Spirobolomyia*, Figs. 350, 352, and 360, all possess semi-sclerous lateral plate-like structures. The affinities of these species are not clear and while the structures will tentatively be considered as homologous with the lateral plates on the basis of their position and structure, more evidence will be needed for confirmation.

HARPES (H)

The harpes are paired antero-dorsal extensions of the corpus. They usually arise at the antero-dorsal corners of the sclerous corpus and run ventro-mesad from there. Their points of origin seem to indicate the primitive antero-dorsal corners of the corpus, even when this has been obscured by subsequent sclerotization.

With one exception, the harpes are present only in the *Sarcophaga* group and their presence is one of the characteristics of that group. In their most simple form, they may be only slightly incurved extensions as in *Sarcophaga misera* Walk., Fig. 128. Zumpt and Heinz (1950), Chart 1, called them the vesica. In others, such as *Sarcophaga tarsata* Ald., Fig. 165, each may be a simple ovate sclerotized lobe. *Sarcophaga thatuna* Ald., Fig. 201, *S. occidentalis* Ald., Fig. 186, and *S. carnaria* (Linn.), Fig. 195, present elongate blade-like harpes. Some more complex forms of this structure are shown in *Sarcophaga nigriventris* Meig., Fig. 178.3, where it is bilobed, and in *Sarcophaga pulla* Ald., Fig. 185, where it forms a large antler-like structure. As can be seen in Figs. 75-214, the harpes are a very variable structure with a tremendous number of observed forms.

Though generally solidly attached, the harpes become articulated in the more advanced forms. A secondary suture is formed at their points of origin. This can be seen in *Sarcophaga pulla* Ald., Fig. 185, and *Sarcophaga carnaria* (Linn.), Fig. 199.

Paraphrissopoda chrysostoma (Wied.), Fig. 290, and *P. gulo* (Fabr.), Fig. 289, also possess what apparently are harpes. In these species the apparent harpes are slightly different in shape, but their general position and points of origin are correct for that structure. Until further evidence

is discovered, they will be called harpes. *Paraphrissopoda hillifera* (Ald.), Fig. 300, possesses a ventral prolongation of the base of the vesica, which might be confused with the harpes. While it resembles the harpes in shape, close examination shows it to be part of the vesica. It is present only in *P. hillifera* and is not given a name.

VESICA (V)

The vesica is the antero-dorsal flap-like appendage of the corpus. It originates as an anterior extension of the membranous area of the corpus and can be seen in its most generalized form in *Camptops unicolor* Ald., Figs. 34 and 36. The vesica in species such as *Sarcophaga pumila* Meig. and *S. arcipes* Pand., Figs. 119 and 124, is also rather generalized. It is from such simple beginnings that the complex sclerotized flap, characteristic of so many of the Sarcophagini, originated. The Agriini seen do not possess a vesica. The developmental process was undoubtedly one of increased flap-like growth followed by sclerotization and then the development of articulation. This process or some variation of it has apparently occurred more than once in the evolution of the Sarcophagini.

The vesica of the genus *Ravinia* is one of the simplest types found. It is a simple depressed flap, slightly expanded distally, Fig. 221. In the genera *Cistudinomyia*, Fig. 286, and *Oxysarcodexia*, Figs. 257-280, it is enlarged and has developed many bizarre variations.

In the *Sarcophaga* group, though very generalized in *Sarcophaga arcipes* Pand., Fig. 124, and a few related species, the vesica has developed into a large and extremely variable structure. As can be seen in Figs. 134, 158, 173, 201, and 206, it is generally bilobed and in a few cases has become split into two parts. This is the case in *Sapromyia cooleyi* (Park.), where it has become two ovate, ventrally spinose lobes, Fig. 97, and in *Sarcophaga haemorrhoidalis* (Fall.), where it has become divided into two separate elongate and divergent lobes, Fig. 210. In *Sarcophaga gracilis* Ald. two similar lobes can be seen with the intermediate sclerotization still present, Fig. 206.

The vesica reaches what is perhaps its peak of bizarre development in *Boettcheria*, in particular *Boettcheria latisterna* Park., Fig. 346. Here it is the dominant element of the phallus.

The plate-like anterior sclerotization of *Rafaelia rufiventris* Tns., Fig. 310, does not have the typical appearance of a vesica but on the basis of its position may represent a very poorly developed vesica. The connate, plume-bearing anterior structure of *Metoposarcophaga*, Figs. 324-335, is also probably a vesica. Its position is correct for a vesica and it can be separated from the specialized corpus.

Most of the members of the *Johnsonia* group and all the Agriini lack a vesica. The vesica in *Johnsonia (Emblemasoma) erro* (Ald.), Fig. 45,

probably represents an independent development, and *Camptops unicolor* Ald. has only a rudimentary vesica, Fig. 36.

EXPLANATE VESICA (EV)

This structure is developed in the Servaisiina, particularly in the genera *Servaisia* and *Fletcherimyia*. Like the vesica it has developed from the membranocorpus, but in a different manner. The membrane probably developed first a slight anterior flap-like projection, as in the early stages of the development of the vesica. Unlike the development of the vesica, the membrane below has next expanded laterally and then ventrally. The result is the structure characteristic of many species of the subtribe Servaisiina, Figs. 366-441. There was undoubtedly some variation in the exact sequence and extent of these developments.

The process in *Fletcherimyia* was probably similar but with greater antero-dorsal growth and further sclerotization than that in *Servaisia* and *Acandotheca*. This resulted in the well-developed explanate vesica characteristic of that genus, Figs. 366, 367, 372, 374, and 375.

In some members of the genus *Acandotheca* an antero-ventral projection of the corpus is present. This is the rudimentary explanate vesica. It is attached near its apex to the modified ventral sclerotization (limen), Fig. 427. In *Acandotheca* (*Acandotheca*) *masculina* (Ald.) it is at right angles to the corpus, Fig. 435; and in *Acandotheca* (*Acandotheca*) *prohibita* (Ald.), Fig. 436, it is turned upward in an arc. *Acandotheca* (*Acandotheca*) *eleodis* (Ald.) and *Acandotheca* (*Acandotheca*) *complosa* (Rein.), Figs. 437, 438, and 444, possess a rather well-developed and complex explanate vesica, probably developed as a continuation of this tendency. The close relationship of these four species as shown by their general aedeagal structure lends validity to this hypothesis.

The tendency for the development of the explanate vesica is characteristic of the Servaisiina. It has developed in the subgenera *Acandotheca*, *Lepyria*, and *Stenolaucotheca* of *Acandotheca*; in the subgenus *Protodexia* and the other subgenera of *Servaisia*; and in *Fletcherimyia*.

Other morphological evidence indicates that these three genera arose from a common ancestor which lacked an explanate vesica; and the development of the explanate vesica in each, apparently, was independent.

The homology of the vesica of *Acandotheca* (*Mecynocorpus*) *salva* (Ald.), Fig. 420, is questionable in view of its apparent relationship, but the structure will be called a vesica here until more evidence is available.

JUXTA (J)

This is the ventral appendage of the corpus. Its development was probably first as a slight bowing out of the ventral membrane of the corpus, as in *Camptops unicolor* Ald., Fig. 36, followed by apical extension

until it appears to be continuous with the corpus as in *Servaisia* (*Servaisia*) *coloradensis* (Ald.), Fig. 383. This is followed by sclerotization and further modification. It is generally bilobed, Figs. 50, 57, 61, 96, and 403.

In the *Sarcophaga* group there is no sharp distinction between those species in which the juxta is fused and those in which it is freely movable. Rather, there seems to be a gradual transition from one condition to the other, with some species such as *Sarcophaga tarsata* Ald., Fig. 167, and *Sarcophaga sima* Ald., Fig. 61, having a fused juxta; some, such as *Sarcophaga thatuna* Ald., Fig. 201, *Sarcophaga occidentalis* Ald., Fig. 186, and *Sarcophaga carnaria* (Linn.), Figs. 195 and 196, having a partially free juxta; and others, such as *Sarcophaga misera* Walk., Fig. 128, and related species, having a free juxta. With one or two exceptions the juxta is freely articulated in those groups, other than the *Sarcophaga* group, in which it is present.

In both the *Sarcophaga* and *Johnsonia* groups the juxta is generally trough- or scoop-shaped, Figs. 36, 45, and 48. There are many specialized variations present, however, as can be seen in Figs. 41, 58, and 69. Dorsally toward its caudal end the juxta of both these groups bears a prow-like median process. Basally the juxta may develop lateral processes as seen in *Sarcophaga misera* Walk. and related species, Figs. 125, 128, 131, 135; in *Helicobia rapax* (Walk.), Figs. 57 and 58; and in *H. stellata* (Wulp), Figs. 61 and 62.

The juxta in the subtribe *Servaisiina* is bilobed with the lobes spatulate in *Servaisia*, Figs. 385, 396, and 398; short and broad in *Fletcherimyia*, Figs. 366, 367; and pointed in *Acandotheca*, Figs. 428 and 435. In the subgenus *Acridophaga* of the genus *Acandotheca* the juxta is completely separated into two parts, Fig. 403. The cope (see p. 17) have developed caudally on the juxta of *Acandotheca* (*Acandotheca*), Figs. 428, 432, 435, and 436.

Among the species of the *Sarcodexiina* examined, *Sarcodexia lambens* (Wied.) bears what is apparently an extremely specialized juxta, Figs. 302 and 304.

The juxta of *Metoposarcophaga* is either fused as in *Metoposarcophaga* (*Zygastropyga*) *cantenea* (Roback) and *M. villipes* (Wulp), Figs. 326, 335, or free and small in *Metoposarcophaga* (*Zygastropyga*) *aurea* (Tns.) and *M. sulculata* (Ald.), Figs. 329 and 317. In both *Rafaelia* and *Boettcheria* it is free, but is much larger and well developed in *Boettcheria*, Figs. 340 and 342. In this group the anterior juxtal process is present.

In *Ravinia effrenata* (Walk.) a scoop-like juxta has formed and the median process has moved ventrad and become attached to it, Figs. 227 and 229. There is no juxta developed elsewhere in the *Raviniina* or in the *Agriini*.

The copi and lateral and anterior juxtal processes have all developed from the juxta (see Chart 2).

LATERAL JUXTAL PROCESSES (LJ)

These are a pair of rods extending laterally and forward from the base of the juxta. They are first developed as membranous lobes, Fig. 113, then become sclerotized and undergo some modification as shown in Figs. 117, 120, 124, and 125. In their sclerotized form they are present only in the *Sarcophaga* group. *Helicobia rapax* (Walk.), Figs. 57-59, and *H. stellata* (Wulp), Figs. 61 and 62, have membranous lateral juxtal processes.

The short membranous flaps developed in *Metoposarcophaga* (*Zygastropyga*) *cantenea* (Roback), Fig. 336, and *Boettcheria carata* Roback, Fig. 345, are probably lateral juxtal processes but the homology is by no means certain.

The lateral processes on the juxta of *Sarcophaga incisilobata* Pand., Fig. 180, are undoubtedly not lateral juxtal processes. Their forward origin and close basal proximity do not support their homology with the lateral juxtal processes of the *Sarcophaga* group. They are specialized structures present only in this species and are not given a name.

ANTERIOR JUXTAL PROCESS (AJ)

This is a generally well-sclerotized semi-tubular process developed dorsally at the antero-median edge of the juxta. It is present only in species of the subtribe Boettcheriina, Figs. 335, 340, 342, and 345, and is apparently associated with the well-developed elongate median process of that group.

VENTRAL SCLEROTIZATION (VS)

This is the third of the three sclerotized areas present in the hypothetical sarcophagine phallus. It consists of a pair of transverse sclerites developed in the membrane of the corpus. Its lateral ends are usually attached to the ventral corners of the sclerous part of the corpus from which point each arm runs medially and then anteriorly, both arms meeting at the mid-line. The ventral sclerotization in *Spathiophora cincta* Loew fits this description exactly, Figs. 7 and 8 (also Chart 3, hypothetical 1) which illustrates the ancestral condition of this part.

The ventral sclerotization undergoes a different development in each of the major lines of the Sarcophaginae. Chart 2 shows the structures (stemmatis, median process, lateral arms, limen, cunabula, lateral and median dorsal projections, median filaments) which have developed from it, while Chart 3 shows the mode of development in each line.

MEDIAN PROCESS (MP)

In two of the lines of development of the ventral sclerotization, a split takes place near the median end of each of its arms, Chart 3 (hypothetical 2 and *M. sulculata*).

In Series 2, this split takes place before the ventral sclerotization has undergone any modification. This results in a two-piece median section and two long lateral arms, Chart 3 (hypothetical 2). The two-piece median section fuses to form the median process, Fig. 26. It is never found in its primitive form.

In the Boettcheriina, the median ends of the ventral sclerotization have become joined and prolonged into a median process and the lateral arms have developed into the lateral filaments, Chart 3 and Fig. 311, before the above mentioned split takes place. The split then results in the free and well-formed median process and lateral filaments of the Boettcheriina, Figs. 319, 340, and 343.

The median process of the Sarcophagulina, Raviniina, Hystricocnema, and Boettcheriina remains a relatively free, generally semi-tubular structure, Figs. 238, 239, 260, and 266, while in the Sarcophagina it forms a prow-like structure, Figs. 64, 69, 133, and 136, attached dorsally to the juxta.

In the genus *Ravinia* it is associated with the dorsal rods. It lies ventro-caudal in the corpus of the more generalized species of that genus, Fig. 219, but moves upward with the lower end of the dorsal rods, Figs. 231 and 233, becoming a little more trough-shaped in the process. It retains a membranous connection with the apex of the corpus, Fig. 233. In *Oxysarcodexia*, Figs. 259 and 260, it also moves upward but becomes more elongate and is associated with both the dorsal rods and the lateral arms. In *Cistudinomyia*, Figs. 285 and 286, only the lateral arms are present with it and it has remained short after its upward movement.

As previously mentioned, the development in the Boettcheriina is slightly different from that in Raviniina. In Boettcheriina the split does not take place until after the median process and lateral filaments are well formed. The median process, here, is generally associated with the apical juxtal process which apparently forms a ventral point of support for it, Figs. 342 and 349. The well-developed triad of tubular median process and well-developed filaments is characteristic of the subtribe Boettcheriina.

In the *Sarcophaga* and *Johnsonia* groups the median process has become attached dorsally to the caudal end of the juxta, Fig. 207. Only in *Arachnidomyia* is it forward. *Ravinia effrenata* (Walk.), though not related to these groups, may illustrate the method of this fusion. In *Ravinia effrenata* the short, tubular median process is attached along its

ventral edge to the dorso-caudal end of a relatively generalized juxta, Figs. 227 and 229. From this the next step would be for the median process to lean farther backward and become completely attached along its lateral and dorsal margins. This would result in the typical median process of the *Sarcophaga* and *Johnsonia* groups, Figs. 46, 49, and 146.

The attached median process gives rise dorsally to the sclerous or membranous capitis in the *Sarcophaga* group, Chart 2 and Figs. 121 and 168.

CAPITIS (CA)

This is the cap or helmet-like structure developed dorsally on the median process of the *Sarcophaga* group and *Helicobia*. It is either sclerous, Fig. 163, or membranous, Fig. 133, the development of each apparently being independent. More evidence is needed to clarify this point. In its most generalized form the capitis appears dome-like in profile, Fig. 64, but tends to become elongate anteriorly, Fig. 155; and in the genus *Wohlfahrtiopsis* it has become partially detached at its base, Fig. 87. The same development has apparently taken place in *Helicobia* as illustrated by *Helicobia morionella* (Ald.), Fig. 54, and *Helicobia rapax* (Walk.), Fig. 59. The median piece in the genus *Spirobolomyia*, Fig. 355, may be a detached capitis but the homology is doubtful.

LATERAL ARMS (LA)

The lateral arms are the outer parts of the ventral sclerotization separated by the median process, Chart 3, hypothetical 2. Only *Cistudinomyia cistudinis* (Ald.), Fig. 285, and *Sarcophagula femoralis* (Schin.), Fig. 26, show this in relatively unmodified form. The apparent lateral arms in *Wohlfahrtia vigil* (Walk.), Fig. 18, may represent the entire ventral sclerotization since there is no indication of the presence of a median process.

In the subtribes Sarcophagina and Boettcheriina and the genus *Oxysarcodexia* they give rise to the lateral filaments, Chart 3 (hypothetical 3, 6, and *O. ventricosa*). They also develop rather complex variations in *Oxysarcodexia*, Fig. 260.

In *Ravinia* they give rise to the dorsally projecting hillae, Chart 3 (*R. stimulans*), and Fig. 226, and then apparently become membranous as there is no indication of their presence after the median process has moved upward, see Charts 2 and 3 (hypotheticals 2, 3, 5, and *R. stimulans*).

LATERAL FILAMENTS (LF)

These are a pair of narrow tubular structures lying one on each side of the median process. They are developed from the lateral arms of the ventral sclerotization as is shown in *Rafaelia rufiventris* Tns., Fig. 311,

and on Chart 3 (hypothetical 3, *O. ventricosa*, and hypothetical 6). In *Camptops unicolor* Ald., Fig. 33, the developed and separate filaments are clearly attached to the ventral tips of the corpus.

The filaments of the *Sarcophaga* group generally consist of an elongate semi-tubular rod and a heavy circular base, Figs. 130 and 137. The bases are usually situated laterally within the corpus, with the rods projecting antero-ventrally, Figs. 173 and 178. In some cases the entire filament may be semi-tubular, Fig. 197, while in others it is expanded distally, Fig. 68.

Both the genera *Rafaelia* and *Metoposarcophaga* have rather short filaments with only a slightly enlarged base, Figs. 311 and 319, but in *Boettcheria* and *Helicobia* the filaments become rather elongate and thread-like with a large base, Figs. 346 and 56.

In *Oxysarcodexia* the modified lateral arms give rise to a pair of anteriorly projecting rods which lie on either side of the median process, Figs. 260 and 270. They are free only in *Oxysarcodexia galeata* (Ald.), Figs. 258 and 259. These are probably homologous with the lateral filaments of other *Sarcophagini*.

DORSAL RODS (DR)

These dorsally projecting rods, Chart 3 (*R. stimulans* and *R. therminieri*) and Figs. 216 and 223, are developed in the membrane of the corpus on either side of the median process in the genera *Ravinia* and *Oxysarcodexia*. At their dorsal ends, they are attached to the base of the vesica, Fig. 250, and these points of attachment act as the fulcrum for the upward movement of the median process.

The structures in *Boettcheria* which resemble dorsal rods, Figs. 240 and 342, are not attached to the base of the vesica and their homology and nature are not known.

HILLAE (HI)

These are well-sclerotized dorsal projections of the lateral arms and are present only in the genus *Ravinia*. In *Ravinia stimulans* (Walk.), *R. latisetosa* Park., and *R. laakei* (Hall), Figs. 217, 220, 226, they are broadly attached, but as the median process has moved up they have drawn away from the lateral arms, Chart 3 (*R. stimulans* and *R. therminieri*) and Figs. 231 and 233, though retaining a connection to them. This connecting strap also moved upward, Fig. 233. The hillae in the more specialized species of *Ravinia* have become a pair of movable sausage-like lobes, Fig. 233.

The lateral dorsal projections of *Fletcherimyia*, Fig. 370, and *Agria affinis* (Fall.), Fig. 13, are probably homologous with the hillae.

The median filaments, the limen, the cunabula and the stemmatis are all developed directly from the ventral sclerotization without any sub-

division of that structure. Though given different names because of their great difference in shape, they are homologous structures. Chart 3 (servasiine and sarcodexiine lines) shows the development of these parts.

LIMEN (L)

This structure is characteristic of the genus *Acandotheca*. It was apparently developed as is shown in Chart 3 (hypothetical 8, 9, and A. *alcedo*), by an anterior prolongation and expansion of the lateral ends of the ventral sclerotization and the antero-ventral prolongation of the median tips. Its generalized structure is most clearly shown in *Acandotheca* (*Acandotheca*) *alcedo* (Ald.), Figs. 425 and 427. In many species it has developed spines, Fig. 435, or hairs, Fig. 432, laterally or has become specialized in other ways, Figs. 437 and 441, but the fundamental structure can be detected in all cases.

CUNABULA (CU)

As in the case of the limen, this structure was derived from the unmodified ventral sclerotization, Chart 3 (*S. coloradensis*, hypothetical 7, *S. opifera*, and *S. aculeata*). It is characteristic of the genus *Servaisia*. The first step in its development was probably the swinging forward and laterad of the median edges of the ventral sclerotization, very much like the opening of a pair of barn doors. The subgenus *Servaisia* illustrates this stage. The next step was the turning inward of the lower point of the median edge until the two lower points met on the mid-line as in *Servaisia* (*Protodexia*) *hunteri* (Hough), Fig. 382. This "rolling under" process continued until the ventral edges of both halves of the ventral sclerotization met on the mid-line. The cradle-like structures found in *Servaisia* (*Acridophaga*) *aculeata* (Ald.), *S. reversa* (Ald.), *S. caridei* (Brèthes), and *S. angustifrons* (Ald.), Figs. 398, 399, 406, and 402, illustrate the completed process.

MEDIAN FILAMENTS (MF)

These filaments, characteristic of the Sarcodexiina, greatly resemble the lateral filaments, but the evidence indicates that their origin was different. The median filaments are formed by the antero-ventral prolongation of the median edges of the ventral sclerotization, Chart 3 (hypothetical 4, *P. amoena* and *E. australis*). In *Paraphrissopoda capitata* (Ald.), *P. amoena* (Ald.), and *P. hillifera* (Ald.) the lateral regions of the ventral sclerotization can still be seen, Figs. 293, 298, and 300, and the median filaments are rather short. However, in *Paraphrissopoda gulo* (Fabr.), *P. chrysostoma* (Wied.) and in *Euboettcheria australis* Tns., where the median filaments are long, these lateral regions are not clearly present.

STEMMATIS (ST)

This wreath-like structure is characteristic of the genus *Fletcherimyia*. It was developed by the formation of lateral dorsal projections on the ventral sclerotization, Chart 3 (*F. jonesi*). The lateral dorsal projections become expanded in *Fletcherimyia jonesi* (Ald.) and *Fletcherimyia celarata* (Ald.) forming a hood-like cap over the median dorsal projections, Figs. 370 and 376. The original ventral sclerotization is no longer clearly recognizable.

LATERAL AND MEDIAN DORSAL PROJECTIONS (LDP AND MDP)

These are dorsal projections of the ventral sclerotization. The median dorsal projections are apparently developed only in the genus *Fletcherimyia*, Figs. 370 and 376. Lateral dorsal projections are also developed in *Agria affinis* (Fall.), Figs. 11-13, and the hillae of *Ravinia*, Fig. 226, although arising from the separated lateral arms, are probably homologous with the lateral dorsal projections of *Fletcherimyia* and *Agria affinis* (Fall.).

COP1 (CO)

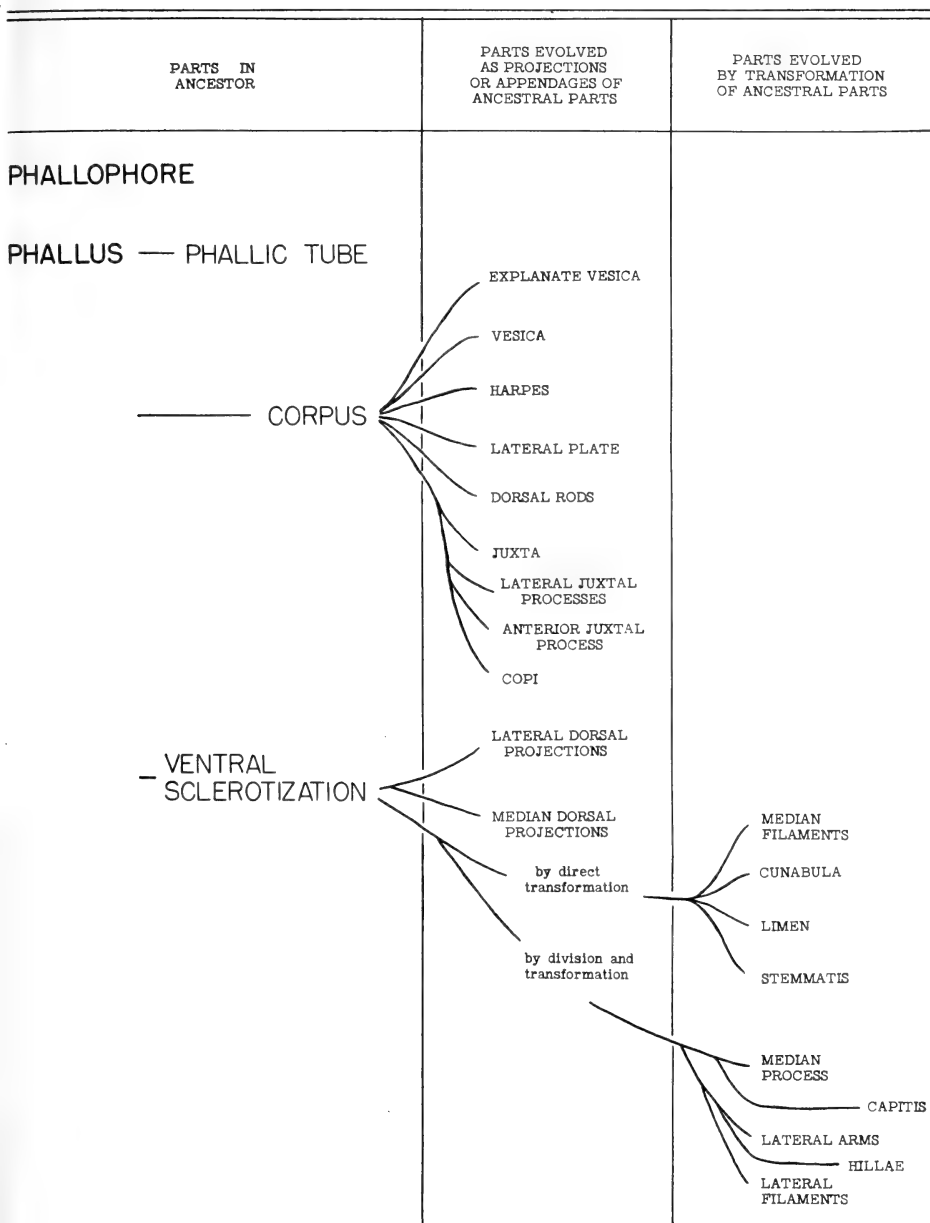
The cop1 are paired, sword-like caudal projections of the juxta in the genus *Acandotheca*. They are generally elongate and movable, being set in the membrane of the juxta, Figs. 428, 432, and 434. The similar structures in *Metoposarcophaga* (*Metoposarcophaga*) *importuna* (Walk.) are sclerous and fused to the juxta, and slightly different in position, and are not considered homologous with the cop1.

CHART I
COMPARATIVE CHART OF THE TERMINOLOGY USED BY VARIOUS AUTHORS
FOR
THE GENITALIA OF SARCOPHAGINAE

AUTHOR	ZUMPT & HEINZ 1950	CRAMPTON 1942	SÉGUY 1941	SENIOR-WHITE 1940	HALLOCK 1940	ROHDENDORF 1928 & 1937	JOHNSTON & HARDY 1923 & HARDY 1943
Anterior & Posterior Claspers	Anterior & Posterior Parameres	Anterior & Posterior Gonapophysis	Gonapophyse Antérieure et Postérieure	Anterior & Posterior Claspers	Anterior & Posterior Claspers	Vordere u hintere Parameren	
Ninth Sternum	Tergosternum	9 Sternum		Paraphallus	Ninth Sternum	Ninth Seg.	
Anal Plates	Paralobi	Surstyli	Forceps Externe	Paralobes	Anal Plate	Forceps In- feriores— Coxite	
Anal Forceps	Cerci	Cerci	Forceps Interne	Superior Claspers	Anal Forceps	Forceps Superiores— Cerci	
Phallopore	Theca	Phallopore	Théca	Hypophallus		Théca	
Corpus	Harpesbasis			Juxta		Pars Basalis— Paraphallus	Sheath
Harpes	Harpes		Paraphallus ?	Appendage of Juxta		Styli	Lobe
Vesica	Vesica— Membran- ulobi		Hypophallus	Vesica		Ventrallobi— Membran- ulobi	Anterior Appendage
Explanate Vesica						Lobi Ventrals	
Juxta	Juxta		Prépuce	Harpe		Pars Distalis— Apikallobi	Apical Process
Lateral Juxtal Processes	Process of Juxta		Piece Terminal du Penis				Lateral Process
Lateral Filaments	Harpes—Proc- ess of Juxta		Styilet du Paraphallus	Median Appendages			Filament
Limen							
Capitis						Pars Interior	Inner Process

CHART 2

EVOLUTION OF SARCOPHAGINE AEDEAGAL STRUCTURES



III. Phylogeny

Roback (1951) postulated the origin of the Sarcophagidae and Calliphoridae from the most primitive of the families of the muscoid calyptrate Diptera, the Anthomyiidae. This was on the basis of evidence drawn from both the larvae and adults. The Anthomyiidae, consisting of two subfamilies, the Anthomyiinae and the Scopeumatinae, were placed in the superfamily Muscoidea in the classification proposed. Both these subfamilies are mostly saprophagous and coprophagous in nutrition.

In the present work the careful examination of the aedeagi of one of the subfamilies of the Sarcophagidae, the Sarcophaginae, indicates that the Sarcophaginae probably arose from the ancestors of the more primitive of the two subfamilies of the Anthomyiidae, the Scopeumatinae. The members of this subfamily are mostly dung feeders and possess a very generalized chaetotaxy. The aedeagi of some extant Scopeumatinae, such as *Scopeuma stercorarium* (Linn.), Figs. 2-5, and *Sapthiophora cincta* Loew, Figs. 6-8, are very close in form to some of the more primitive Sarcophaginae, such as *Camptops unicolor* Ald., Figs. 34-36.

The other subfamily of the Sarcophagidae, the Miltogramminae, is not considered here, but the aedeagi examined, as in Fig. 9, and seen in the literature, Allen (1926), Patton (1939), indicate that it could have arisen from the same ancestor as the Sarcophaginae.

On the basis of a consideration of the morphology of extant Sarcophaginae and Scopeumatinae, the following characters are postulated for the archetype of the Sarcophaginae:

Head, Thorax, and Abdomen

1. Arista bare.
2. Proclinate fronto-orbitals present on head in male.
3. Frontal rows, of head bristles, parallel.
4. Two notopleurals.
5. Two posterior dorsocentrals.
6. Three or four hypopleurals.
7. Scutellum with only laterals.
8. Abdomen without macrochaetae.
9. Membrane between fifth and seventh abdominal segments short.
10. Hind tibiae bare.
11. First and fifth veins bare.

Genitalia

1. Phallic structure simple, Fig. 1.
2. Ventral sclerotization and phallic tube present.
3. Phallopore and phallus articulated.
4. Fifth sternite simple, Fig. 10.
5. Sixth sternite not attached to fifth.
6. Anal plates large, clasper-like, Fig. 5.

Nutrition

1. Coprophagous or saprophagous.

MORPHOGENETIC EVOLUTION

From the above ancestor, two major lines, the tribes Agriini and Sarcophagini have arisen, Chart 3. In the former, the fifth sternite has remained simple, Fig. 6; the membrane between the morphological fifth and seventh abdominal segments has remained short; the frontal rows are parallel or gradually divergent; and the sixth sternite has remained free of the fifth. In the Sarcophagini, the fifth sternite is V- or Y-shaped, Figs. 35, 60; the membrane between the morphological fifth and seventh abdominal segments has become elongated; the frontal row is generally slightly divergent in the lowest bristles; and the sixth sternite has become attached to the fifth.

On the basis of its retention of so many of the features of the archetype, the Agriini can be considered the more primitive of the tribes.

AGRIINI

The subtribes Wohlfahrtiina, Sarcophahrtiina, and Agriina constitute the tribe Agriini, Chart 3. Each is monogeneric.

In *Wohlfahrtia* and *Sarcophahrtia* the phallus has partially or entirely closed over, Figs. 15, 18, and 19, and the ventral sclerotization has not developed any projections; but in *Agria* the phallus is completely open ventrally, and the ventral sclerotization has developed large lateral dorsal projections, Figs. 11-13. Each of the genera exhibits its own specializations, and without the examination of more specimens it is difficult to determine definitely the most generalized and specialized members of this tribe.

Agria on the basis of the open corpus could be considered the most generalized, while *Wohlfahrtia*, on the basis of the well-formed ventral closure and its habit of human myiasis, is probably the most specialized. *Wohlfahrtia* is the most widely distributed of all three genera, being found in all regions but the Neotropical and Australian (see Chart 3).

Superficially the aedeagus of *Wohlfahrtia vigil* (Walk.), Fig. 19, resembles that of many members of the genus *Ravinia*, Fig. 243. Parker

(1914b) thought that this indicated relationship between the two. However, a close examination of aedeagal structure shows that this is a case of convergence of form between two widely separated genera.

SARCOPHAGINI

The tribe Sarcophagini is, both in number of species and individuals, the larger of the two subtribes of the Sarcophaginae, and the phylogeny of its components constitutes the major part of this discussion. The phylogeny of the three series within it, and the subtribal and generic components of each series will be explained. This phylogeny is shown graphically on Charts 3-9.

The archetype for the Sarcophagini differs from that for the Sarcophaginae in the following characters:

1. Arista plumose.
2. Frontal rows, of head bristles, generally slightly divergent below.
3. Membrane between the morphological fifth and seventh abdominal segments long, Text Fig. 1.
4. Fifth sternite V- or Y-shaped.
5. Sixth sternite attached to fifth.

Within the Sarcophagini there are three major lines of development, Series 1, 2, and 3.

Series 1 consists of the monogeneric subtribe *Impariina*. The genus in turn consists of only the very aberrant species *Imparia impar* (Ald.). The asymmetrical phallus and the large flaring phallic tube, Figs. 20-22, are unique within the Sarcophagini. On the basis of the large phallic tube it is considered the most primitive of the subtribes.

Series 2 consists of the subtribes Sarcophagulina, Hypopeltina, Hystriocnemina, Chart 3; Sarcophagina, Charts 4 and 5; and Raviniina, Chart 6. In all of these the ventral sclerotization has formed a median process and lateral filaments, Fig. 26, which have generally undergone subsequent modification. On the basis of the large number of species with coprophagous and saprophagous nutrition and the more primitive chaetotaxy of some of its species, Series 2 is considered more generalized than Series 3.

Series 3 consists of the subtribes Sarcodexiina, Chart 7; Boettcheriina, Chart 8; and Servaisiina, Chart 9. The ventral sclerotization has undergone direct modification or has split into three parts after modification, Chart 3, Boettcheriina line.

The generally parasitic or predaceous habits of the members of this Series, the fact that there are never less than three posterior dorsocentrals, and the absence of proclinate fronto-orbitals in the males place this as the most specialized of the three Series.

As far as can be determined from the morphological evidence, all three originated from a common ancestor. The relationships and phylogeny of the subtribes will be discussed under the Series headings and the generic relationships and phylogeny under the subtribal headings.

Series 2

In the subtribe Sarcophagulina, Chart 3, the lateral arms are barely modified, Fig. 26, and have not moved, Fig. 27. There is no juxta present and the fifth sternite is small and weakly indented, Figs. 24 and 28. Proclinate fronto-orbitals have been retained in the male and there are only two notopleurals. The vesica is large and rather specialized, Figs. 25, 29. All this supports the primitive position accorded this subtribe. It is undoubtedly the most generalized of the subtribes of Series 2.

The two species (*S. femoralis* (Schin.) and *S. occidua* (Fabr.)) included in the Sarcophagulina have generally been placed in separate genera, *Sarothromyia* and *Sarcophagula*, respectively. However, the similarity of phallic structure and overall external characters between the two species do not support this distinction, and they are both included in the genus *Sarcophagula*.

SARCOPHAGINA

In the subtribe Sarcophagina, the ventral sclerotization has developed into the median process and lateral filaments, Chart 3. The median process has fused to the juxta, Fig. 102, which is present in all genera of this subtribe except *Argoravinia*.

Although the Sarcophagina contains some very primitive genera and species, it is probably one of the most specialized of the subtribes of Series 2. Many of its species are parasitic and have even become human parasites. The phalli of many species are very specialized.

Within this subtribe two large generic groups are recognized. The members of the more generalized of the two, the *Johnsonia* group, Chart 4, generally lack a well-developed vesica and have generally retained a vestige of the phallic tube, Figs. 41, 44, 49. They may have as few as two posterior dorsocentrals and two notopleurals. The membrano-corpus is often well developed, Figs. 36, 41. The genera *Camptops*, *Chloronesia*, *Argoravinia*, *Johnsonia*, and *Helicobia* are included here.

On the other hand, the genera of the *Sarcophaga* group, Chart 5, always have at least a small vesica, never have a phallic tube, and do not have less than three posterior dorsocentrals and four (sometimes apparently three) notopleurals. The corpus here is generally well developed and sclerotized, Fig. 167. The genera *Sarcomyia*, *Sapromyia*, *Arachnidomyia*, *Wohlfahrtiopsis*, and *Sarcophaga* are placed here.

JOHNSONIA GROUP

The genus *Camptops*, though possessing a vesica, Fig. 36, must have evolved rather early. The presence of only two notopleurals, proclinate fronto-orbitals on the male of *C. unicolor* Ald., the highly membranous phallus, Fig. 36, and the small, weakly indented fifth sternite, all support such a conclusion.

The genus *Harpagopyga* has been separated from *Camptops* on external chaetotaxy, but the phalli of the two are very close morphologically, and the two genera are here combined as the genus *Camptops*.

The genus *Chloronesia* here includes the genus *Notochaeta*. These two have been combined, as were *Camptops* and *Harpagopyga*, on the basis of the morphological similarity of the male phallus.

Though some of its species may have as few as two posterior dorso-centrals and two notopleurals, *Chloronesia* is accorded a higher position than *Camptops*, Chart 4, on the basis of the larger and better developed sclerocorpus, Fig. 41, and the well-developed fifth sternite, Fig. 42. Also, proclinate fronto-orbitals are not present in the male.

The placement of the genus *Argoravinia* is a tentative one. Its phallic structures, Figs. 38, 39, do not show any clear relationship to any other Sarcophagini seen, and it is placed here on the basis of the shape of the sclerocorpus and the relatively large membranocorpus. Its phallus bears some resemblance to that of *Chloronesia*.

The genus *Johnsonia*, as used here, is a combination of the genera, *Johnsonia*, *Emblemasoma*, and *Sthenopyga*. The genitalia of all three, Figs. 44, 45, 48, are too close structurally to admit of generic separation. The well-developed vesica of *Emblemasoma*, Fig. 45, merits subgeneric recognition for it.

The juxta in *Johnsonia* is well developed and sclerotized in contrast to the lightly sclerotized juxtae in *Camptops* and *Chloronesia*, Figs. 36, 41. The lateral plates, Figs. 44, 45, 48, have developed in the membranocorpus and there is very little membranous area left in the phallus. There are three or four posterior dorsocentrals. The phallus of *Johnsonia* is more advanced than that of *Camptops*, *Chloronesia*, and *Argoravinia*.

The subgenus *Johnsonia* provides the probable point of origin for the genus *Helicobia*, Chart 4. The depressed juxta, Figs. 44, 62, the lateral plates, Figs. 48, 58, the lack of a vesica, the barely divergent frontal row, and three posterior dorsocentrals are common characters to both. The juxtae of *Johnsonia* (*Johnsonia*) *rufitibia* (Wulp), Fig. 50, and *Helicobia rapax* (Walk.) are very similar in ventral view.

Helicobia has developed a ribbon-like lateral filament, Fig. 56, and has lost the phallic tube completely. The capitis is developed here and has become almost completely detached in *Helicobia rapax* (Walk.), Fig. 59. *Helicobia australis* J. and T., although not a typical *Helicobia*,

is tentatively placed here until its affinities can be more definitely established, Figs. 63-66. *Helicobia* is the most specialized genus of the *Johnsonia* group.

SARCOPHAGA GROUP

The *Sarcophaga* group probably arose early from the *Johnsonia* group stock, Chart 4. Its closest affinities in the *Johnsonia* group are to the genus *Camptops*. The form of the lateral filaments and corpus is similar in both. The *Sarcophaga* group could not have been derived from any of the genera above *Camptops*. The fifth sternite of all these genera has a well-developed window, Figs. 42, 43, 47, 51, 60, while the most generalized members of the *Sarcophaga* group lack the window, Figs. 103, 107, and could not have arisen from these genera.

The genus *Sarcomyia*, though possessing a rather specialized phallus, Figs. 79, 80, must have been an early offshoot of the *Sarcophaga* line, Chart 5. The bare hind tibiae, relatively simple fifth sternite with few hairs and no window, the poorly developed median process and lack of a capitis, all indicate an early origin for this genus. The phallus of the only species placed in it, *S. scelestus* (Hall), shows no clear relationship to that of any other Sarcophagini seen.

Arachnidomyia, Chart 5 and Figs. 67-78, though it also lacks the hair on the hind tibiae, is more advanced than *Sarcomyia* on the basis of the well-developed median process and capitis, Fig. 69. Also, the fifth sternite possesses a window. *A. aldrichi* (Parker), though possessing thin lateral filaments, Fig. 78, and a more depressed juxta than the other members of this genus, Figs. 76, 77, is included here on the basis of the position and shape of the median process, Fig. 77, the resemblance of its harpes to those of *A. houghi* (Ald.), Figs. 76, 75, and the bare hind tibiae.

The placement of the genera *Sapromyia* and *Wohlfahrtiopsis* is a difficult problem. The shape of the fifth sternite, its elongate base, widely spread arms, and heavy bristles at the base of the V, Figs. 83, 85, 88, 91, 95, and 101, relate the two genera to each other, as does the small, freely articulated juxta of both.

The phallic structures of both are so specialized as to give little evidence as to their relationships to other genera and to their probable point of origin, Figs. 82-102. On the basis of the bare hind tibiae of *Wohlfahrtiopsis*, we can say that it probably arose at a point close to that of *Arachnidomyia*, Chart 5. The genus *Sarcophaga* probably also arose with these two.

The bare hind tibiae of *Wohlfahrtiopsis*, as well as the smaller number of bristles on the fifth sternite, Figs. 83, 85, 88, indicate that it was the first of the two genera to differentiate, Chart 5. Both genera have undergone very rapid evolution and have left no intermediates.

Sarcophaga is the largest and most widely distributed of the genera

of Sarcophagini. Most of its members have the hind tibiae villous and generally have well-developed harpes, median process and capitis, Figs. 103-214. The fifth sternite of the most generalized members of this genus lacks a window, Figs. 103, 107, but possesses a strong brush of bristles. Most of the species have a window in the fifth sternite. The genus probably had a common origin with *Arachnidomyia* and *Wohlfahrtiopsis*, Chart 5. There is no evidence to indicate a later or completely separate origin.

No attempt has been made to divide this genus further into other genera or subgenera. The probable evolution of the species treated here is shown on Chart 5. There is no single point or points where the author felt that good generic or subgeneric divisions could be drawn. The pattern of phallic structure in *Sarcophaga* is basically of the same mold in all, and it is felt that the relationship of the species seen is best expressed by including them in a single genus.

RAVINIINA

The subtribe Raviniina consists of the genera *Ravinia*, *Oxysarcodexia*, and *Cistudinomyia*, Chart 6. The ventral sclerotization shows a tendency to move upward into the corpus after its division, Fig. 243. This is the condition present in all but a few species of the genus *Ravinia*, Figs. 219, 232. A juxta is not present (except in the aberrant *R. effrenata* (Walk.), Figs. 227, 229) and lateral filaments are present only in the genus *Oxysarcodexia*, Figs. 266, 270.

The fifth sternites of all three genera are similar, Figs. 234, 272, 287; and the phallophore and phallus of all three are fused, Figs. 233, 280.

The lack of a juxta indicates that Raviniina must have separated from the sarcophagine line before the development of the juxta in that line, Charts 5, 6. It has developed some very specialized phallic structures, but its food habits are mostly saprophagous and coprophagous. There are few parasites recorded in this subtribe.

Cistudinomyia is probably the earliest offshoot of this line, Chart 6. Although the vesica is very specialized, the relatively unmodified lateral arms and lack of dorsal rods, Fig. 285, indicate that it must have differentiated before either *Ravinia* or *Oxysarcodexia*, both of which possess dorsal rods, Figs. 216, 270. After its separation, the median process and lateral arms moved upward. Its rather specialized habit of parasitism in turtles points to an early origin and subsequent specialization.

The ventral closure, prolongation of the phallus, and the movement upward of the ventral sclerotization seem to be common tendencies in this subtribe. They have occurred in all three genera.

The development of the dorsal rods in the main stock gave rise to the

progenitor of the genus *Oxysarcodexia*. In this genus the phallus is partially closed over ventrally, Figs. 273, 274, and the median process and lateral arms have moved upward, Fig. 269, but not as much as in the genus *Ravinia*, Fig. 252. The lateral arms have developed complex modifications and have given rise to the thin lateral filaments, Fig. 260.

In *Oxysarcodexia galeata* (Ald.), the lateral filaments are present, but the remainder of the lateral arms have apparently been lost, Figs. 258, 259. The projections present on the inner side of the sternal arms, Fig. 256, grow longer in this genus, increasing the depth of the V and pushing the peaks of the lateral arms laterad, Figs. 263, 265, 271. The vesica develops many bizarre variations, Figs. 261, 262, 264, 274.

The development of the hillae from the lateral arms, after the formation of the dorsal rods, would give the prototype for *Ravinia*. *R. stimulans* (Walk.) is not far from this hypothetical type, Figs. 217, 219. In fact, without the hillae and dorsal rods, it would not be far removed from the ancestor for the entire Raviniina.

In *Ravinia*, as in *Cistudinomyia* and *Oxysarcodexia*, the parts of the ventral sclerotization have moved upward and inward. Unlike the latter two genera, the beginning and at least one of the intermediate steps are present here. In *R. stimulans* (Walk.) the hillae are firmly attached, and the median process and lateral arms are ventral in the corpus, Figs. 215-219. In *R. errabunda* (Wulp), Figs. 230-232, the hillae, though still well sclerotized and pigmented, have pulled away from the lateral arms and remain attached to these vanishing pieces by a caudo-ventral band. The median process has moved partially upward into the corpus, and the dorsal rods are no longer vertical. In a species such as *R. therminieri* (R. D.), which represents the end point of this process, Figs. 242-244, the hillae have become light and sausage-shaped. Their connectives are now almost completely horizontal, as are the dorsal rods. The corpus, Fig. 243, is more elongate and more completely closed over than in either *Cistudinomyia* or *Oxysarcodexia*. The upper ends of the dorsal rods are attached to the base of the vesica, Fig. 250, and these points act as the fulcrum for the upward movement of the median process and the lower ends of the dorsal rods.

The fifth sternite shows progressive change as one goes from *R. stimulans* (Walk.), *R. laakei* (Hall), and *R. latisetosa* Park., Figs. 218, 224, 225, where the V is wide, to the higher species of *Ravinia*, where the V has become narrower and deeper, Figs. 234, 235, 239, 242.

The current division of this genus into *Ravinia* and *Chaetoravinia* on the basis of the setulose first vein cannot be accepted when the genitalia are carefully considered. The fact that intermediates, such as *R. errabunda* (Wulp) and *R. dampfi* (Lopes), are present would lend doubt

to the validity of this generic division. The genitalia of these two species are closer to those of *Ravinia*, in the strict sense, but they possess the setulose first vein of *Chaetoravinia*. Since the genitalia show phylogenetic direction while the setulose first vein crops up again and again, it seems better to consider *Chaetoravinia* and *Ravinia*, in the strict sense, as one genus—perhaps in the process of splitting into two genera, but not yet there. Townsend's (1917b) group of splinter genera are not at all tenable.

The remaining two subtribes of Series 2 are the Hypopeltina and the Hystricocnemina, Chart 3. Each consists of a monobasic genus, *Hypopelta* and *Hystricocnema*, respectively. Both are aberrant subtribes and their placement is tentative. Neither genus shows clear relationship to any other known Sarcophagini.

HYSTRICOCNEMINA

H. plinthopyga (Wulp) possesses a tubular median process, and lateral filaments, Figs. 283, 284, which resemble those of *Sarcophaga fulvipes* Macq., Fig. 192. It does not possess juxta, vesica, harpes, or capitis and probably differentiated very early before those structures evolved. The form of the corpus, Fig. 281, anal plates, and anal forceps, Fig. 453, is very specialized.

HYPOPELTINA

Hypopelta scrofa Ald. with its sail-like vesica, odd corpus, Figs. 30, 32, and small filaments, Fig. 31, is a difficult species to place. It shows affinities to both Series 2 and the subtribe Boettcheriina of Series 3, Chart 8. It possesses lateral filaments, but the homology of the median process is very doubtful and is of no help in placing the species.

The small size of the filaments, Fig. 31, suggests an early origin from the base of Series 2, Chart 3, rather than from the subtribe Boettcheriina of Series 3. The lateral filaments of the species placed in the latter subtribe are very much larger than those of *Hypopelta*, Figs. 314, 336, 346, and a great deal of reduction would have to be postulated to arrive at those of *Hypopelta*. Since the lateral filaments, when present, show a tendency to enlarge or elongate, it seems more reasonable to assume that the lateral filaments of *Hypopelta* evolved small and remained small, rather than to assume that they were reduced from those of any extant *Boettcheriina*.

To propose their development from the lateral arms of a common ancestor with the Boettcheriina would involve postulating not only reduction, but also that the split in the ventral sclerotization, after its modification, occurred twice, in separate lines.

Series 3

The three subtribes of Series 3, the Sarcodexiina, Boettcheriina, and Servaisiina, as far as can be seen at present, probably arose from a common ancestor. Each subtribe presents its own specializations and it is difficult to designate any as the most generalized or specialized. Most of the species in all three are parasitic, though a very few saprophagous and predaceous forms are known.

SARCODEXIINA

The subtribe Sarcodexiina of Series 3, Charts 3 and 7, is characterized by possession of median filaments, Fig. 290. It consists of three genera, *Paraphrissopoda*, *Euboettcheria*, and *Sarcodexia*.

Of these three, *Paraphrissopoda* is undoubtedly the most generalized. Though all of its species possess a vesica, Figs. 289, 290, 294, 297, 299, the more primitive members of the genus, *P. amoena* (Ald.), *P. hillifera* (Ald.), and *P. capitata* (Ald.), Figs. 293, 298, 300, still retain the lateral sections of the lateral arms and possess a rudiment of the phallic tube. *Paraphrissopoda* and the *Euboettcheria*-*Sarcodexia* line arose from a common ancestor.

Euboettcheria has developed a specialized elongated corpus, lacks a vesica, and has lost all trace of the lateral sections of the lateral arms, Figs. 305, 307, and phallic tube. It probably differentiated before the development of the vesica.

Sarcodexia, whose phallus also lacks a vesica, bears some resemblance to *Euboettcheria* in the long median filaments and tubular base of the corpus, Figs. 302, 204. It probably differentiated from a common ancestor with *Euboettcheria* and subsequently developed the very specialized bifurcate juxta and its other specialized genital structures, Chart 7.

BOETTCHERIINA

The subtribe Boettcheriina is the only one of Series 3 in which any division of the ventral sclerotization takes place. Unlike Series 2, here it takes place after the median process and lateral filaments have become distinctly formed, Chart 3. Eight genera constitute this subtribe. These are *Rafaelia*, *Metoposarcophaga*, *Aphelomyia*, *Boettcheria*, *Spirobolomyia*, *Kellymyia*, *Cucullomyia*, and *Tylomyia* (see Charts 3 and 8).

The genus *Rafaelia* is the most generalized of this subtribe. It is the only genus in which the lateral filaments and median process are still connected, Figs. 311, 314, though well formed. The structure of the corpus, Figs. 310-313, juxta, and vesica is very simple. *Rafaelia* comes very close to being the ancestor for the subtribe Boettcheriina.

Metoposarcophaga is one of the few genera of Sarcophagini which has

retained large anal plates, Figs. 333, 334, and small anal forceps. Its separation must have taken place early, before the reduction of the anal plates in *Rafaelia*. *Boettcheria* also possesses moderately elongate anal plates, Fig. 450, and short anal forceps. Its origin is close to that of *Metoposarcophaga*, Chart 8.

The corpus, vesica, and phallopore of *Metoposarcophaga* are extremely specialized, Figs. 316, 317. The plume-like vesica and capsule-like corpus are unique within the Sarcophagini.

The subgeneric division within *Metoposarcophaga* is based on both external and genital characters. The presence of only three posterior dorsocentrals, bare hind tibiae, and the more rounded corpus, Fig. 324, places the subgenus *Metoposarcophaga* as the more generalized of the two subgenera. Also, its genital segments do not protrude as much as those of *Zygastropyga*, Fig. 460, and the fifth sternite is simpler, Fig. 321. In the latter subgenus there are four posterior dorsocentrals, the hind tibiae are villous, and the corpus projects caudally, Fig. 316 (see Chart 8).

Boettcheria is a very specialized genus and, as mentioned before, probably arose with, or close to, *Metoposarcophaga*, Chart 8. There is no evidence upon which to separate them. The vesica, Figs. 337, 341, 344, 348, and the lateral filaments, Fig. 346, have become very large and specialized. The frontal row reaches its greatest divergence below in this genus.

The remaining genera of this subtribe are all rather aberrant and unique forms. They show little clear relationship to each other or to any other Sarcophagini and are placed in this subtribe on the basis of the possession of lateral filaments and a free median process and juxta, or on a resemblance to one of the genera mentioned or to one another (*Kellymyia* and *Spirobolomyia*).

Aphelomyia does not possess any of the triad of processes, but its vesica, Fig. 330, bears great resemblance to that of *Metoposarcophaga*, Fig. 327, and it is placed close to that genus.

Spirobolomyia possesses a well-developed triad of median process and lateral filaments, Fig. 355, but the structure of the parts is not identical with those of *Boettcheria* and *Metoposarcophaga*. The species of this genus possess semi-sclerous lateral plates, and the form of the corpus and fifth sternite of all of them is unique, Figs. 352-355.

Kellymyia is placed close to *Spirobolomyia* on the basis of its possession of semi-sclerous lateral plates. The phallus is unique in all other respects and lacks the triad of processes, Figs. 308-309.

Both *Tylomyia* and *Cucullomyia* possess very unusual phalli which show little relationship to those of any other Sarcophagini, Figs. 357, 362. The possession of the triad of processes places them in this subtribe, but their more exact affinities are not ascertainable at present.

SERVAISIINA

In the subtribe Servaisiina, the ventral sclerotization has become modified, but no division has taken place. The three genera definitely placed in it, *Fletcherimyia*, *Servaisia*, and *Acandotheca*, each represent a different modification of the ventral sclerotization, Chart 3. The fifth sternite of all three is very similar, Figs. 369, 391, 430; a juxta is generally present; and there is a tendency for the development of the explanate vesica. When present, this latter structure is characteristic of the subtribe. The point of origin of this subtribe is probably close to that of Boettcheriina and Sarcodexiina, Charts 3 and 9.

Kurtomyia contains only the single aberrant species, *K. postilla* (Rein.), Fig. 410. It is placed in this subtribe on the basis of the similarity of its fifth sternite, Fig. 408, to those of the genera *Servaisia* and *Acandotheca*.

Fletcherimyia is a very distinctive genus of four species, all of which have been reared from the cups of *Sarracenia*. All four species possess the stemmatis, Fig. 370, a large, well-formed explanate vesica, Figs. 366, 367, and a bilobed juxta, Fig. 366. The lobes of the juxta are soft, hairy, short, and apically down-turned, Figs. 366, 367. The stemmatis shows some progressive development within the genus, being larger and better developed in *F. jonesi* (Ald.), Fig. 370, and *F. celarata* (Ald.), Fig. 376, than in *F. fletcheri* (Ald.), Fig. 366.

The development of the cunabula is the distinguishing characteristic of the genus *Servaisia*, Chart 3. A juxta and the explanate vesica are generally present. It consists of the subgenera *Acridophaga*, *Servaisia*, *Sarpedia*, *Protodexia*, and *Speciosia*.

The subgenera *Sarpedia* and *Servaisia* possess the earliest stage in the development of the cunabula, Figs. 385, 368, 389. Here the median tips of the arms of the ventral sclerotization have swung forward, but the "rolling under" process is partially complete, Fig. 382, and in *Acridophaga*, Figs. 402, 403, the process is complete. The sequence of evolution of the subgenera is not linear as above.

The subgenus *Protodexia* lacks any trace of a juxta, Figs. 377, 380, and was probably the first to differentiate, Chart 2. As mentioned above, the cunabula in this subgenus has developed to a point where it probably represents the intermediate condition between the subgenera *Servaisia* and *Acridophaga*.

The subgenus *Sarpedia* possesses a very small juxta, Fig. 389, and could have arisen together with the subgenus *Servaisia*, the juxta in *Servaisia* having undergone subsequent development after the separation of the subgenera, Figs. 392, 396. The structure of the cunabula is similar in both, Figs. 389, 393. One of the species in *Sarpedia*, *S. (Sarpedia) setigera* (Ald.), is the only web-spinning sarcophagid that has been recorded, Branch (1920).

In *Acridophaga* the juxta, basically the same in structure as in *Servaisia*, has completely split at its base, forming two lobes, Figs. 402, 403. This would indicate that it probably developed from *Servaisia* after the juxta was fairly well developed there, Chart 9. The cunabula in *Acridophaga* is fully developed, Figs. 399, 401, 407, and cradle-like. The explanate vesica, present in all members of the subgenus *Servaisia*, Figs. 383-387, 391-396, is also present in all species of *Acridophaga*, but is more pigmented and sclerotized in the latter, Figs. 397-407.

The genitalia of the subgenus *Speciosia* are very aberrant, Figs. 411, 412, 458. The only species, *S. (Speciosia) speciosa* (Lopes), possesses a cunabula similar to that of *Protodexia* and lacks a juxta. It has therefore been placed close to the last mentioned subgenus, Chart 9. Its fifth sternite, Fig. 411, is like that of other members of the genus *Servaisia*.

The genus *Acandotheca* is characterized by the possession of the limen. It has been divided into five subgenera here. These are *Stenolaucotheca*, *Acandotheca*, *Tephromyiella*, *Lepyria*, and *Mecynocorpus*, Chart 9.

The subgenera *Stenolaucotheca*, *Lepyria*, and *Mecynocorpus* all lack a juxta, Figs. 414, 420, 423, while the subgenera *Tephromyiella* and *Acandotheca* possess this structure, Figs. 417, 428. The first three subgenera probably arose before the latter two, but it is impossible to assign any sequence of origin to them, Chart 9. Each presents its own unique specializations.

The juxta in *Tephromyiella* is large and scoop-shaped, Figs. 416, 418, very different from the bifurcate, sharply pointed juxta of *Acandotheca*, Figs. 428, 429. The copi have developed on the juxta of *Acandotheca*, Fig. 435.

All three genera of the *Servaisiina* probably arose from a common ancestor. There is no evidence to show any sequential arrangement of their origins.

As can be seen in the foregoing discussion, genital characters are of great value in determining the phylogeny and relationships within the Sarcophaginae. The external characters and chaetotaxy were found to be of very little value in this regard. They did, however, demonstrate certain tendencies throughout the Sarcophaginae, and the more important of these are listed below.

1. Toward villous hind tibiae.
2. Setulose veins besides the third (first and fifth).
3. Increased abdominal chaetotaxy.
4. Increased divergence of the frontal row, below.
5. Increase in number of hypopleurals.
6. Increase in number of posterior dorsocentrals.

Xenopopia hypopygialis Tns. (equals *Camptopyga aristata* Ald.) was

considered by Aldrich in his "*Sarcophaga* and Allies." The phallus and fifth sternite of this species are very aberrant, Figs. 442-445, and its nearest relatives are apparently in the Amobiini of the subfamily Miltogramminae. *Neophyto setosa* Coq., Figs. 446, 447, is very close to it on the basis of the aedeagus and could be ancestral to *X. hypopygialis*.

CHART 3

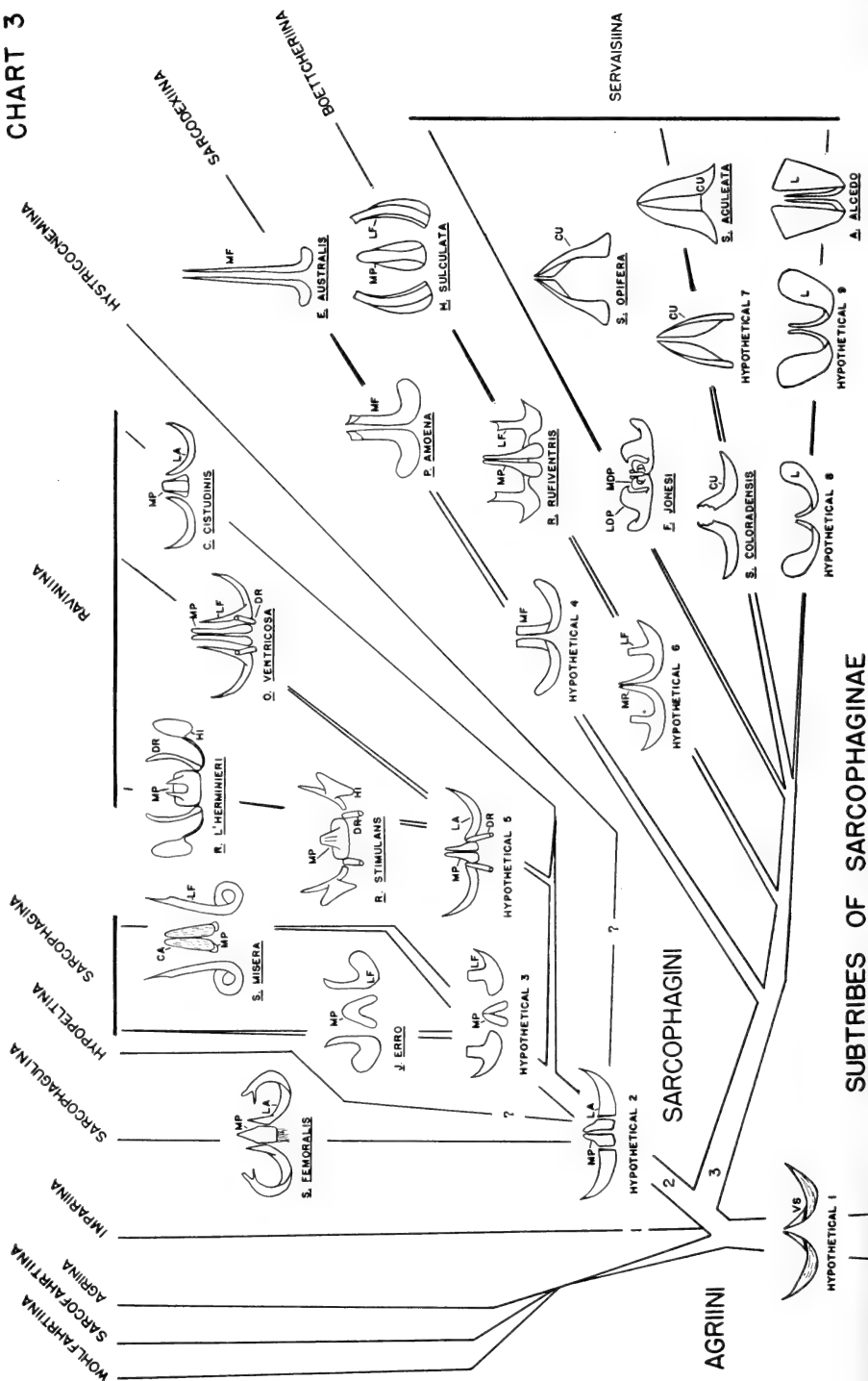
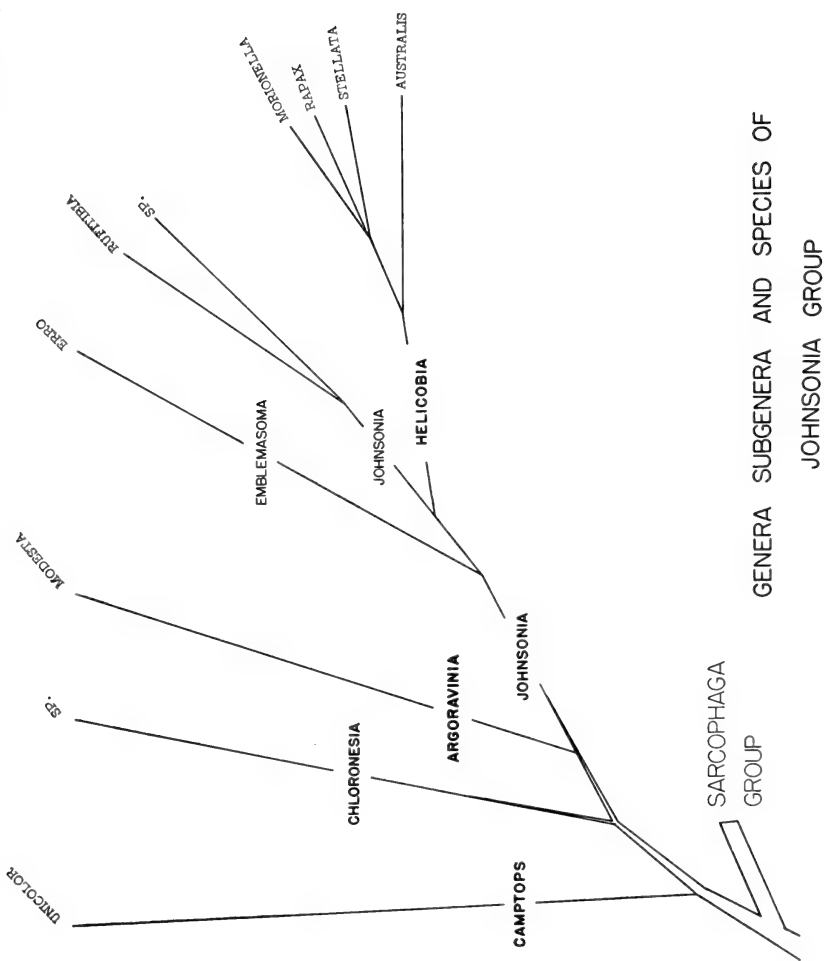
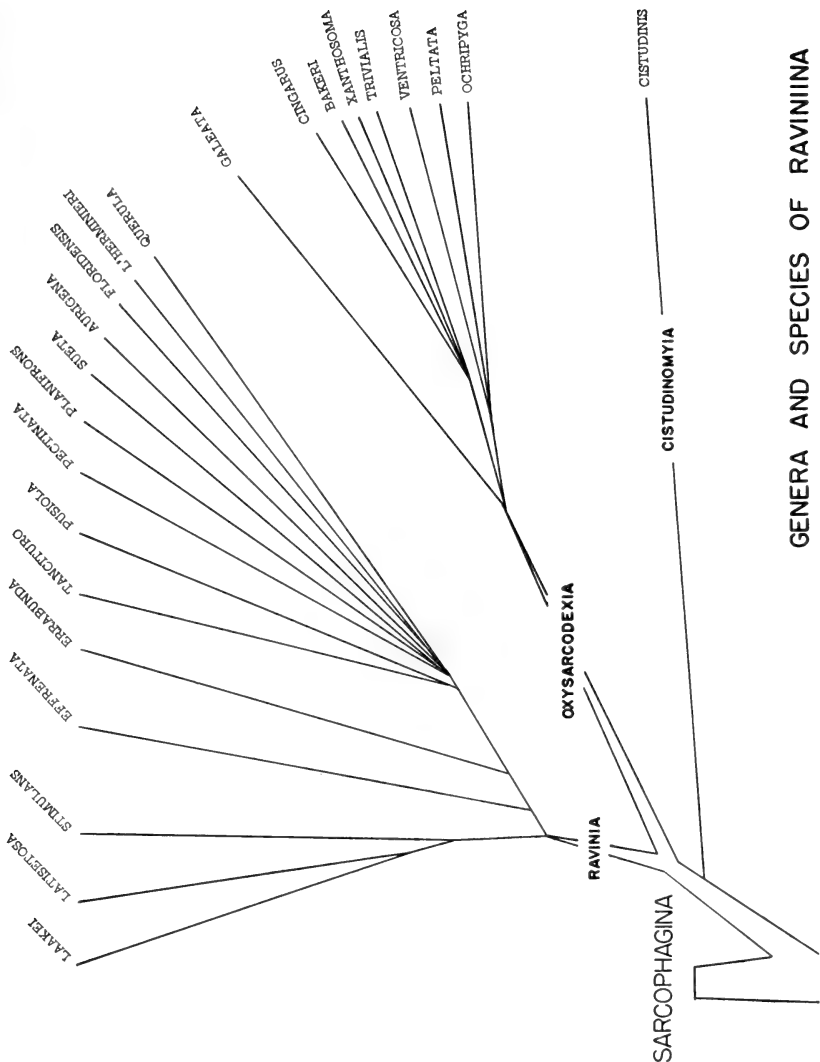


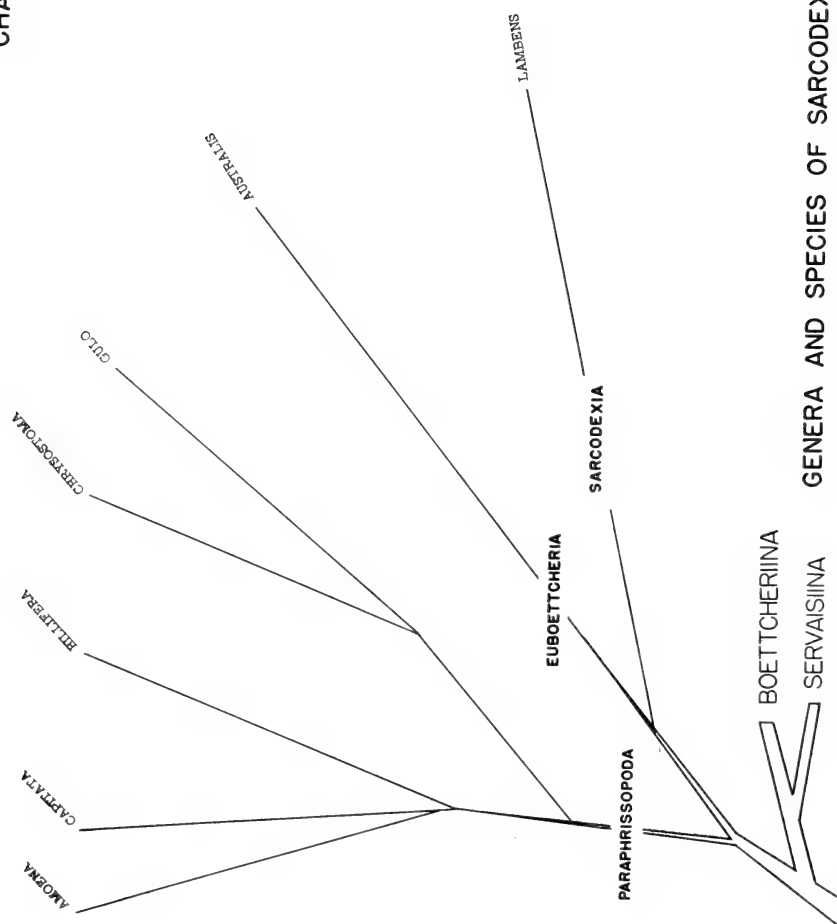
CHART 4

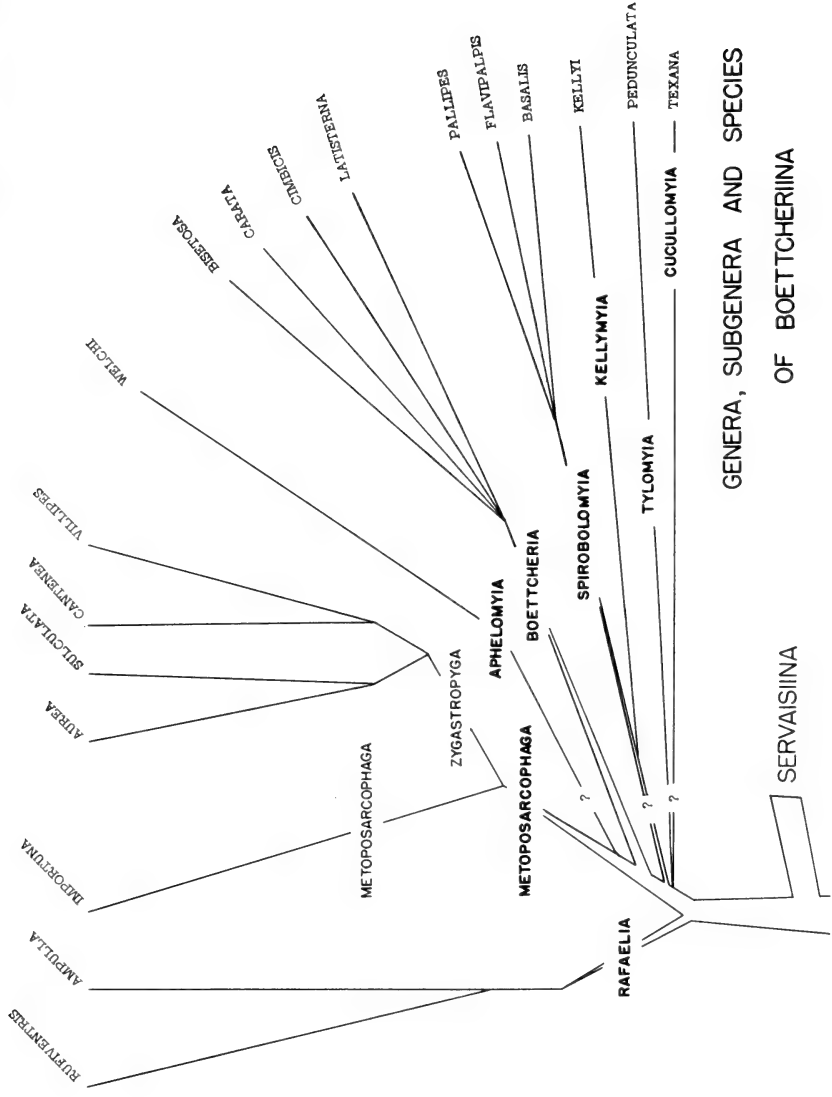




GENERA AND SPECIES OF RAVINIINA

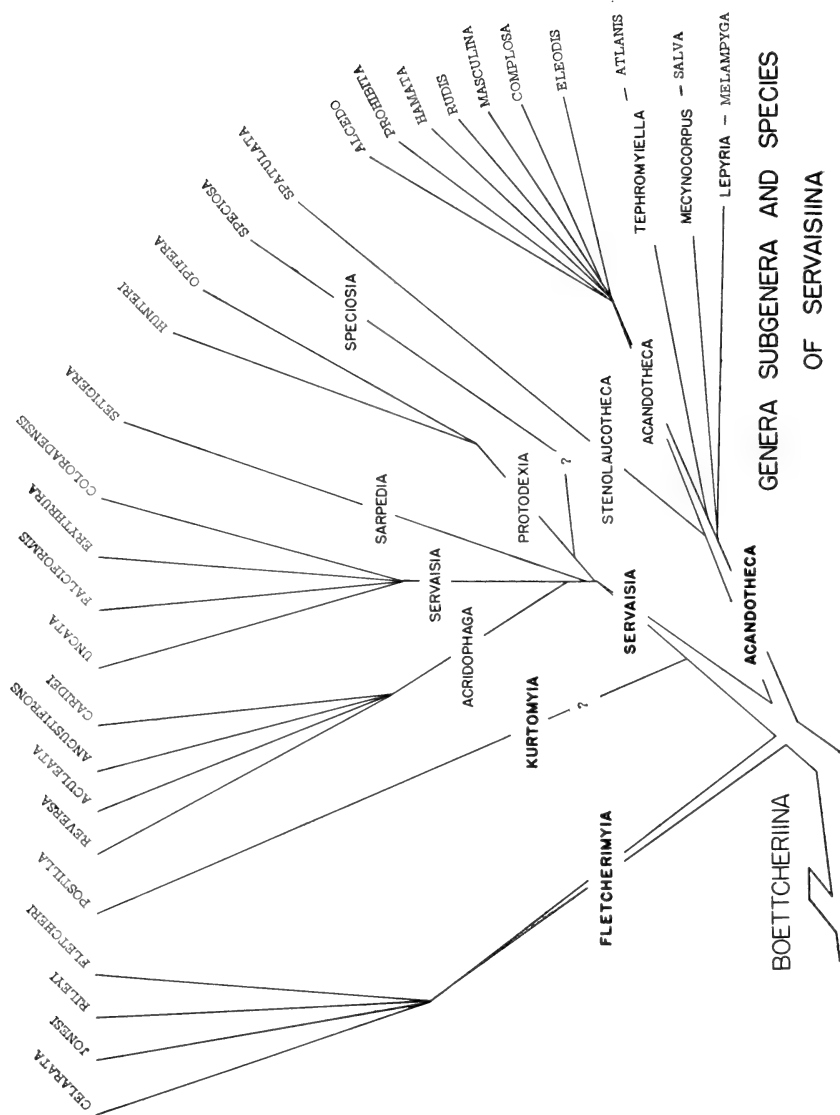
CHART 7





GENERA, SUBGENERA AND SPECIES
OF BOETTCHERIINA

CHART 9



GENERA SUBGENERA AND SPECIES
OF SERVAISIINA

IV. Biogeography

It must be remembered that the conclusions and interpretations expressed here are tentative. Our knowledge of the sarcophagine fauna, though appearing extensive, is still very fragmentary for many parts of the world, and the views expressed here will undoubtedly be modified by the acquisition and consideration of new material.

Only the tribe Sarcophagini will be discussed here. There is too little material available on the tribe Agriini to enable any biogeographic conclusions to be drawn.

Two postulates presented by Ross and King (1951) are applicable here and should be kept in mind throughout the discussion:

1. If many species arise through geographic isolation, the least changed or primitive species should represent those still remaining in conditions most similar to the ancestral habitat; and the most changed should represent phyletic lines which have become adapted to conditions differing most from the ancestral.

2. That morphological change in male genitalia is correlated or associated with physiological change related to habitat.

Both these postulates are elaborated in the above-mentioned paper.

ORIGIN AND GEOGRAPHIC CORRELATION

The most primitive Sarcophagini, those which most nearly approach the hypothetical ancestor in morphological details, are in the Caribbean region, centering around Central America. These are species such as *Camptops diversipes* (Coq.), *C. unicolor* Ald., and both species of *Sarcophagula* and of *Rafaelia*. All are located around the Caribbean. With postulate one in mind, we can therefore assume that Central America represents the area of origin for the Sarcophagini. The ancestral species evolved here and then apparently spread into North and South America.

The North American population of this imaginary ancestor probably gave rise to the subtribe Impariina, represented at present only by a single genus and species, *Imparia impar* (Ald.). This aberrant species is found only in the United States.

The distribution of the primitive members of Series 2 seems to indicate that the series arose in Central America in about the same region as the Sarcophagini ancestor. The primitive members of Series 2, *Sarcophagula* and *Camptops* spp., have changed less from the ancestral form

than the primitive members of either Series 1 or 3, and are distributed around the Caribbean.

The most primitive members of Series 3, *Rafaelia rufiventris* Tns. and *R. ampulla* (Ald.), are distributed in the southern United States and Mexico. The most generalized Sarcodexiina are circum-Caribbean and West Indian in distribution, and the Servaisiina are essentially Palearctic and Nearctic in distribution. All this would indicate southwestern North America or just south of it as the region of origin for Series 3. In the United States and South America, more specialized members of all three subtribes are found.

After its origin, the Series 2 ancestor spread into North and South America. Near its point of origin it gave rise to the progenitor of *Sarcophagula* which has remained restricted to the Caribbean area.

Later, the North American segment gave rise to the lines of the Raviniina. The most generalized members of this subtribe, *Ravinia stimulans* (Walk.), *R. latisetosa* Parker, *R. laakei* (Hall), and *Cistudinomyia cistudinis* (Ald.) are North American and West Indian in distribution. The species of the genera *Ravinia* and *Oxysarcodexia* which arose from this line spread back down into South America and are well represented there by specialized forms. *Oxysarcodexia* is the predominant genus of Sarcophagina in southern Brazil. Existing species of *Cistudinomyia* are restricted to North America.

In northern South America, the Series 2 ancestor gave rise to the ancestor of the Sarcophagina. The most primitive species of the Sarcophagina, *Camptops* spp. and *Chloronesia* spp., are distributed around this area. *Chloronesia* is predominantly a South American genus.

The next step in the evolution of Series 2, apparently, was the spread of the Sarcophagina ancestor into North America. The *Sarcophaga* group arose from it in North America, while the *Johnsonia* group arose from its South American segment.

Up to this point it seems that the populations of these various ancestors and groups had been able to spread up and down the Central American bridge, into North and South America, but now we come to a group which apparently was not able to spread into South America. This is the *Sarcophaga* group. This group is world-wide in distribution at present and is the generally predominant Sarcophagina group. It is, however, very poorly represented in South America, and some of the present records are obviously due to introduction by commerce.

The above fact, plus the presence of many generalized forms of the *Sarcophaga* group in North America, suggest this area as the place of origin of the group.

The most primitive members of the *Johnsonia* group are predominantly

South American and seem to indicate that the *Johnsonia* group arose there. Northern South America is probably the area of origin.

As postulated previously, the present distribution of the species of Series 3 indicates that southwestern North America represents the ancestral habitat and probably also the point of origin for the Series. From this area the ancestor of Series 3 spread into South America.

The most primitive existing Boettcheriina are located in the southern United States and Mexico, and on this basis we can likewise assume that this was the area in which the Boettcheriina arose. This subtribe has since spread into the northern United States and Canada, and down into South America. It is represented by several specialized genera in North America.

The Sarcodexiina, on the other hand, probably arose in Central America or northern South America. The most primitive species of the subtribe, those of the genus *Paraphrissopoda*, are located in Central America, northern South America, and the West Indies. A few species have been recorded from Florida. From this distribution we can infer that this subtribe arose in the south Central America or northern South American area. Specialized species of this subtribe are found southward into Chile and northward into the southern United States.

The area of origin of the Servaisiina cannot be definitely placed at present. Insufficient material was seen or was available in the literature to make possible the assignation of the Servaisiine ancestor to any specific area. Its primarily northern distribution, Nearctic and Palearctic, does suggest that it arose in the Northern Hemisphere.

The above conclusions have been drawn on the basis of the material examined and those species which could be definitely placed on the basis of figures or descriptions in the literature. There is a need for more collection and study—especially in the Ethiopian and Australian regions. The sarcophagine fauna of both these regions is far from well known, and a better understanding of the integration of their fauna with that of the rest of the world would add much to our understanding of the origin and distribution of the Sarcophagini.

There are so many groups whose center of origin seems to be Central or South America, that it seems possible to suggest that they arose after the period in the Cretaceous when there was free interchange of sub-tropical faunas between the New and the Old World. This would give a lower limit to the origin of these groups.

The several alternating periods of free interchange and isolation between North and South America during the Cenozoic undoubtedly contributed to speciation and the differentiation of groups.

If this were true, it would indicate that most of the genera of the Sar-

cophagini were of Miocene origin or even later, which would make them relatively young as compared to some of the more primitive insect groups. It would not, however, preclude the possibility that a few arose in the Oligocene or even earlier.

At what time the Sarcophagini became a world-wide northern group is not clear—it was perhaps in the Eocene or Miocene. The *Sarcophaga* group with its broad distribution and abundant fauna is perhaps the key to this problem. It must be examined and considered on a world-wide basis and the details of its evolution worked out.

V. Nutritive Evolution

As can be seen from a perusal of the records in the literature, the Sarcophaginae have a great variety of nutritive habits. These range from saprophagous and coprophagous to human parasitism, very often within a single species. For example, *S. sarracenioides* has been reared from garbage and as a parasite of grasshoppers, and *S. haemorrhoidalis* from dung, as a parasite on insects, and as a human intestinal parasite. These examples are not unique in the Sarcophaginae. Most of the major lines of the Sarcophaginae show a great range of nutritive habits and are not specialized in any particular way. The Wohlfahrtiina and the Servaisiina are exceptions to the above statement. The members of the Wohlfahrtiina are, as far as known, all parasitic on a great variety of animals, while most of the Servaisiina are parasites of grass-land Orthoptera. Only the *Sarracenia*-dwelling members of *Fletcherimyia* are exceptions to this. The females of the parasitic Servaisiina have developed a spatulate ovipositor not found in other Sarcophaginae. It is interesting to note that in spite of the diversity of nutritive habits, the eggs and larvae of the Sarcophaginae are remarkably uniform in their morphology.

When we compare the nutritive habits and the lack of distinctive egg and first instar larval types in the Sarcophaginae with the nutritive habits and egg and first instar larval types in such entirely parasitic groups as the Larvaevoridae and Parasitoid Hymenoptera, we can see that the Sarcophaginae are, ecologically, what might be called a transition group, undergoing the change from coprophagous and saprophagous nutrition to pure parasitic nutrition.

Both the Larvaevoridae and Parasitoid Hymenoptera are entirely parasitic and have developed specializations not present in the Sarcophaginae. The Larvaevoridae have developed four egg types and three first instar larval types, and the Parasitoid Hymenoptera have developed five egg types and fourteen first instar larval types. As mentioned before, the eggs and first instar larvae of the Sarcophaginae are so similar throughout that no types have been distinguished. The reproductive capacity of the members of the Sarcophaginae is lower than that of either of the other two groups.

There are many vertebrate groups whose fossil record indicates that they have undergone a change in nutritive habit. A few examples will

illustrate the change in nutrition and the corresponding morphological changes.

The horse in 60,000,000 years, from *Hyracotherium* to *Equus*, has changed from a browser to a grazer. This change has been accompanied by changes in dentition, skull proportions, etc.

The perfection of the carnivorous habit from the Creodonts to the extant Carnivora in about 69,000,000 years was accompanied by great changes in the teeth and head.

Among the reptiles, the Procolophonids, in changing from a carnivorous to a herbivorous habit (30,000,000 years), underwent such changes as:

1. Shortening of the lower jaw.
2. Loss of teeth.
3. Formation of teeth into opposed grinding chisels.

Still more examples could be cited to show that in vertebrate evolution a change in food habit is accompanied by morphological change in the animal.

If our estimates of the age of the Sarcophaginae is correct, it has been evolving for about 45 to 70 million years, about as long as most of the above groups. In all this time, through all the fossil forms which must have existed, the Sarcophaginae have failed to develop any morphological change in the mechanism of food intake to correlate with the change in nutritive habit they are undergoing. The egg, larvae, and adult show no significant changes. The male aedeagus has changed (see plates), and we depend on this for our species groupings and phylogeny, but these changes have not always kept pace with food habit changes. We are, therefore, led to assume that the change in the Sarcophaginae must be physiological rather than morphological. This is not to imply that no physiological change has taken place in the vertebrates. Both have taken place there.

The Sarcophaginae, in retrospect, present the picture of a group—emerging at the end of the Cretaceous—evolving with diverse aedeagal forms and into a great range of food habits, without any correlated change in feeding apparatus of either larvae or adults but probably with great physiological change.

VI. Classification

The classification of the Sarcophaginae presented in this section is based upon the opinions and conclusions drawn in regard to the phylogeny of the species treated here and the homology of their phallic structures.

No attempt has been made to write keys to the larger phylogenetic groupings used in this paper. They are large, broad groupings which do not lend themselves to easy key construction. Instead, a synopsis of tribes and subtribes has been prepared to show the important characters and relationships of the larger groupings. It is not a key for the identification of specimens. Also, a key to all the new and old genera (based on males) which are treated here has been constructed.

In the key to genera, external characters have been used as much as possible. However, in some groups the external features do not offer any good key characters, and male genital characters have been used. The genital characters, though more difficult to use, are more reliable than external characters and are the final arbiters in doubtful cases.

The key is primarily designed to separate the genera occurring in the Nearctic region, but Neotropical material belonging to the genera treated here will in most cases key out satisfactorily.

The descriptions are based mostly on specimens seen.

LISTS AND ABBREVIATIONS

After each generic or subgeneric description there is a list of the species included in it. After the species name, authority, and date there are letters indicating the general distribution of the species and whether that species has been seen by the author or is definitely or tentatively placed in that genus on the basis of figures or descriptions in the literature. The last column contains a citation to the paper in which a good figure or description of the species can be found. The following abbreviations will be used.

S—Seen by author.

D—Definitely placed on the basis of good figure or description in the literature.

T—Tentatively placed on the basis of evidence in the literature.

Distribution:

A—Australian region.

E—Ethiopian region.

O—Oriental region.

Oc—Oceanic region.

Ne—Nearctic region.

No—Neotropical region.

P—Palearctic region.

SYNOPSIS OF TRIBES AND SUBTRIBES—MALES

1. Fifth sternite entire, Figs. 10, 16, 17, membrane between morphological fifth and seventh abdominal segments short; arista pubescent or short plumose **Agriini**—2
 Fifth sternite V- or Y-shaped, Figs. 35, 43, 85, membrane between morphological fifth and seventh abdominal segments long; arista long and plumose **Sarcophagini**—4
2. Abdomen with median and lateral shining spots; spots sometimes slightly confluent; phallic tube reduced; Figs. 17-19; arista pubescent **Wohlfahrtiina**
 Abdomen not as above; generally pollinose; phallic tube well developed, Figs. 13, 14; arista short plumose 3
3. Corpus rounded apically, Fig. 14; ventral sclerotization not clearly defined; phallic tube may be very long, Fig. 14; costal spine present **Sarcophahrtiina**
 Corpus extended anteriorly at apex, Fig. 13; ventral sclerotization greatly enlarged; phallic tube about one-half as long as above, Fig. 13; costal spine absent **Agriina**
4. Phallus asymmetrical; large phallic tube present, Figs. 20-23. **Impariina**
 Phallus not as above; phallic tube, if present, much reduced and not easily seen 5
5. Ventral sclerotization undergoes direct modification; no division... 6
 Ventral sclerotization undergoes division, forms 3 parts 7
6. Limen, Figs. 419-420, cunabula, Figs. 384, 390, 406, and stemmatis, Figs. 366-370, formed, except *A. postilla* (Rein.); corpus tubular and generally short; fifth sternite with window and short base; female with spatulate ovipositor; explanate vesica generally present; 3 or 4 posterior dorsocentrals; anterior acrosticals generally present; scutellars 2 or 3-1-1; * hind tibiae bare; third abdominal segment with median marginals, see Figs. 366-441 **Servaisiina**
 Median filaments formed; corpus, if tubular, greatly elongate; fifth sternite with long narrow arms; vesica may be present; female not

* Scutellar bristles are given in the following order: lateroscutellars—discoscutellars—apicoscutellars.

- with spatulate ovipositor; hind tibiae generally villous; 4-6 posterior dorsocentrals; anterior acrosticals generally absent; see Figs. 289-307 **Sarcodexiina**
7. Large median process and spinose lateral filaments formed; fifth sternite without window; very wide and shallow; anal forceps, in lateral view, bipronged vertically; anal forceps as wide or wider than high; 5 posterior dorsocentrals; see Figs. 281-284. . **Hystricocnemina**
Not with above combination of characters 8
8. Phallus almost horizontal; boat-shaped; juxta small and partially concealed; lateral filaments and median process very small; vesica fused, turned upward; sail-like; 3 posterior dorsocentrals; no anterior acrosticals, Figs. 30-32 **Hypopeltina**
Phallus and lateral filaments and median process not as above; vesica generally free 9
9. Two notopleurals; fifth sternites small and shallowly notched; lateral arms barely modified; no juxta; large vesica; proclinate fronto-orbitals present in both sexes; genitalia as in Figs. 24-29 **Sarcophagina**
Two to 4 notopleurals; fifth sternite generally larger and more deeply notched; lateral arms modified; if simple they have moved upward; juxta present or absent; proclinate fronto-orbitals generally present only in females 10
10. Juxta absent, except *R. effrenata* (Walk.); phallus and phallopore fused; corpus partially or entirely closed over ventrally; dorsal rods present in *Ravinia* and *Oxysarcodexia*; 3-5 posterior dorsocentrals; anterior acrosticals generally present; apical scutellars generally absent; Figs. 215-280, 285-287 **Raviniina**
Juxta present; phallus and phallopore generally free; corpus not closed over ventrally; lateral filaments and median process present 11
11. Median process fused to juxta; division of ventral sclerotization takes place before modification; capitis, harpes, small sclerous lateral plates, and a rudimentary phallic tube may be present; 2 to 6 posterior dorsocentrals; Figs. 33-214 **Sarcophagina**
Median process free; division takes place after modification; capitis and other parts above, never present; 3 to 5 posterior dorsocentrals; genitalia as in Figs. 308-365 **Boettcheriina**
- The above synopsis shows the characters and relationships of the tribes and subtribes of Sarcophaginae. It is not for identification of specimens.

KEY TO GENERA—MALES

1. Fifth sternite entire; membrane between morphological abdominal segments 5 and 7 short; arista bare or pubescent 2

- Fifth sternite V- or Y-shaped; membrane between morphological fifth and seventh abdominal segments long, Text Fig. 1; arista generally plumose4
2. Abdomen with three rows of black spots; spots may be confluent, Fig. 448 **Wohlfahrtia**
 Abdomen with grey and black checkered pattern, tessellated; pattern shifting with light angle..... 3
3. Costal spine present but small; phallic tube may be long, Fig. 14; anal plate and forceps distant from each other, Fig. 449, or anal plate may appear fused to ninth tergum **Sarcophahrtia**
 Costal spine absent; phallic tube short; ventral sclerotization very large; Figs. 11-13 **Agria**
4. First vein bare5
 First vein setulose35
 First and fifth veins setulose **Johnsonia** (pt.)
5. Aedeagus asymmetrical; large phallic tube present, Figs. 20-23; anal forceps as in Fig. 451 **Imparia** n. gen.
 Aedeagus symmetrical; large phallic tube not present6
6. Anal forceps bipronged vertically, Fig. 453; prongs equal in length; forward prong with hook; aedeagus as in Figs. 281-284.....
 **Hystriocnema**
 Anal forceps not bipronged as in Fig. 453; if slightly bipronged, prongs are never equal, Fig. 456, and anterior prong not with sharp black hook7
7. Posterior lateral clasper black, tubular, turned outward; anterior clasper with ventral row of bristles; phallus as in Figs. 30-32.....
 **Hypopelta**
 Posterior lateral clasper not black and tubular; generally turned anteriorly, never outward; anterior clasper not with ventral row of bristles; phallus not shaped as in Figs. 30-328
8. Large patches of yellow-brown hair below latero-scutellars; phallus as in Figs. 362-365 **Cucullomyia** n. gen.
 No such patches of hair present; phallus not as above9
9. Genital segments large and protuberant, Fig. 460; abdomen may have truncate appearance caudally; anal plates generally large, may be longer than anal forceps, Fig. 334; phallus smooth and capsule-like, Figs. 316, 327-336; phallopore extended hook-like, caudally, at base **Metoposarcophaga** (pt.)

- Genital segments not large and protuberant as above; anal plates generally smaller, oval or triangular in shape; never longer than anal forceps; phallus not shaped as above10
10. Phallus generally turned caudad from phallophore; corpus smooth, small, barrel-shaped; vesica plume-like; Figs. 330-332
..... **Aphelomyia** n. gen.
Phallus not generally turned as above; corpus not small, smooth and barrel-shaped; vesica not as above11
11. Phallus of type shown in Fig. 41; lateral arms of fifth sternite with mesal expansions, beginning about half way to apex and tapering to apex, Fig. 42; oral vibrissae at oral margin; abdomen with metallic sheen; 2 or 3 posterior dorsocentrals **Chloronesia**
Phallus not as in Fig. 41; if lateral arms with mesal expansions [(*J. (Emblemasoma) erro*] then oral vibrissae above oral margin and approximated; abdomen not with metallic sheen12
12. Two notopleurals; third abdominal segment with row of bristles; fifth sternite small and weakly indented, Fig. 2413
Three or 4 notopleurals; fifth sternite larger and more deeply indented, Fig. 4714
13. Discoscutellars present; vesica large and distinct; juxta absent; abdominal stripes black; phallus, Figs. 24-29 **Sarcophagula**
Discoscutellars absent; vesica membranous, not large; juxta present; abdominal stripes brown; phallus, Figs. 34-36 **Camptops** (pt.)
14. Oral vibrissae above oral margin, approximated; genitalia as in Figs. 45-47 **Johnsonia** (pt.)
Oral vibrissae at oral margin; genitalia not as above15
15. Frontal row very strongly divergent in last 4 or 5 bristles; 3 posterior dorsocentrals; anal forceps short; generally with basal tuft of hair; anal plate generally inverted L-shaped, Fig. 450; Figs. 337-349.....
..... **Boettcheria**
Frontal row not as above; if strongly divergent, then 4 to 6 posterior dorsocentrals present; anal forceps not as above16
16. Phallophore and phallus fused; phallus partially or entirely closed over ventrally; apical scutellars generally lacking17
Phallophore and phallus free; phallus not closed over ventrally; apical scutellars generally present19
17. Third abdominal segment with marginal row of 20 bristles; anterior acrosticals barely differentiated; genitalia, Figs. 286-287.....
..... **Cistudinomyia**

- Third abdominal segment with median marginals at most; anterior acrosticals generally well differentiated18
18. Vesica simple, flap-like; hillae present; genitalia, Figs. 233-255....
 **Ravinia**
 Vesica large and complex; hillae absent; genitalia, Figs. 256-280...
 **Oxysarcodexia**
19. Juxta large and forked, Fig. 302; gives phallus appearance of inverted Y; median filaments present **Sarcodexia**
 Juxta not forked as above20
20. Juxta with caudally projecting copi, Figs. 428-441; anal forceps as in Fig. 456 **Acandotheca** (pt.)
 Copi not present, if juxta is present21
21. Anal forceps short; reverse L-shaped, Fig. 458; bulbous at bend of L; corpus with lateral hooks at apex; paired semi-sclerous plates present on each side of corpus; cunabula present; Figs. 411-412....
 **Servaisia** (pt.)
 Anal forceps not as above; corpus not with hooks22
22. Stemmatis present; juxta consists of a pair of large, soft, light-colored and delicately haired lobes; explanate vesica large and well sclerotized; stemmatis often projecting anteriorly; Figs. 366-376.....
 **Fletcherimyia**
 Stemmatis not present; juxta not as above; explanate vesica, if present, not as large and more membranous23
23. Anal forceps variably indented at base, Fig. 456; tip turned forward; generally some spines or hairs at bend; corpus semi-tubular; variable in length; cunabula or limen present; explanate vesica may be present24
 Anal forceps not as above; corpus not semi-tubular; cunabula and limen not present26
24. Large scoop-shaped juxta present; bears large limen dorsally; Figs. 416-418 **Acandotheca** (pt.)
 Juxta, if present, not shaped as above25
25. Short tubular limen present at tip of corpus; higher than wide with hook below; appears as a vertically placed rectangle in profile; explanate vesica present; Fig. 414 **Acandotheca** (pt.)
 Limen not present; juxta, if present, bifurcate with spatulate tips or completely divided at base, Figs. 384, 386, 392, and 403, 406; cunabula present; membranous explanate vesica generally present; Figs. 380-407 **Servaisia** (pt.)

26. Corpus, in lateral view, thin and blade-like; curved forward apically; partially or completely bifurcate at apex, Figs. 308, 309, 410. 27
Corpus of various shapes; never blade-like in profile 28
27. With large vertically ovate plates present on either side of corpus; anal forceps sharply hooked near tip, Fig. 452; Figs. 308-309.
. **Kellymyia**
Lateral plates not present; forceps not as above; divided vesica present; Fig. 410 **Kurtomyia** n. gen.
28. Corpus large; hooked apically; shaped as reversed K; large, foliate, semi-sclerous lateral plates present; Figs. 350-361. . . . **Spirobolomyia**
Corpus not shaped as above; lateral plates not present. 29
29. Corpus and juxta continuous in contour, forming a claw-shaped structure; vesica bent vertically at its mid-point; Figs. 79-81.
. **Sarcomyia** n. gen.
Corpus not shaped as above 30
30. Vesica consists of two ovate ventrally spinose lobes; Figs. 90-102; juxta small and free **Sapromyia** n. gen.
Vesica, if divided, not spinose as above 31
31. Median filaments present; fifth sternite with long arms and a short sternal base; juxta absent; posterior dorsocentrals 3 small—2 large; discoscutellars generally lacking 32
Median filaments not present; fifth sternite generally with longer base; juxta present; 3 to 6 posterior dorsocentrals; discoscutellars generally present 33
32. Vesica present; corpus robust; Figs. 288-301 **Paraphrissopoda**
Vesica absent; corpus elongate, tubular at base; Figs. 305-307.
. **Euboettcheria**
33. Vesica large and of bizarre shape; as long as corpus; capitis elongate, projects from within corpus; almost detached from median process; anal forceps stout with brush of hair on outer side near tip, Fig. 459; corpus often coated with yellow mass, Figs. 82-89. . . **Wohlfahrtiopsis**
Vesica and capitis not as above; anal forceps without brush near tip; yellow mass not present 34
34. Hind tibiae bare; harpes never blade-like; juxta short and broadly attached to corpus; median process placed anteriorly on juxta; capitis generally sclerous; 3 or 4 posterior dorsocentrals, Figs. 70-77.
. **Arachnidomyia**
Hind tibiae generally villous; harpes may be elongate and blade-like or very large; median process placed posteriorly on juxta; capitis

- membranous or sclerous; 3 to 6 posterior dorsocentrals; Figs. 103-214.....**Sarcophaga**
35. Two notopleurals; male with proclinate fronto-orbitals; genitalia, Figs. 34-36.....**Camptops** (pt.)
- Three or 4 notopleurals; male without proclinate fronto-orbitals...36
36. Phallus and phallopore fused; hilla present; Figs. 211-231.....**Ravinia** (pt.)
- Phallus and phallopore separate; hilla absent.....37
37. Genital segments large and protuberant, Fig. 460; abdomen may have truncate appearance caudally; anal plates generally large, may be longer than anal forceps, Fig. 334; phallus smooth and capsule-like, Figs. 316, 327-336; phallopore extended hook-like, caudally, at base.....**Metoposarcophaga** (pt.)
- Genital segments not large and protuberant as above; anal plates generally smaller, oval or triangular in shape; never longer than anal forceps; phallus not shaped as above.....38
38. Second abdominal segment with median marginals; limen and explanate vesica present; Figs. 422-424.....**Acandotheca** (pt.)
- Second abdominal segment without median marginals.....39
39. Lateral plates present, Figs. 48, 52, 58; no vesica present.....40
- Lateral plates not present; vesica may be present.....41
40. Apical scutellars present; third abdominal segment generally with median marginals or a complete row; phallic tube absent; Figs. 52-62.....**Helicobia** (pt.)
- Apical scutellars absent; without median marginals on third abdominal segment; phallic tube present; Figs. 48-51.....**Helicobia** (pt.)
41. Juxta thin and elongate in lateral view; corpus with pair of long lateral ribbon-like processes; Figs. 63-66.....**Helicobia** (pt.)
- Juxta heavier; corpus not with pair of long lateral ribbon-like processes.....42
42. Frontal row broadly divergent in last three bristles; anal forceps strongly hooked in profile, Fig. 457; genitalia, Figs. 419-421.....**Acandotheca** (pt.)
- Frontal row barely divergent in last bristle; anal forceps not shaped as above.....43
43. Three posterior dorsocentrals.....**Rafaelia**
- Four posterior dorsocentrals.....44

44. Anal forceps reddish-yellow, short, Fig. 455; free part directed ventro-caudad; Figs. 37-39 **Argoravinia**
 Anal forceps black, long; tip curved anteriorly, Fig. 454; short white hairs on either side of scutellum below lateroscutellars; Figs. 356-359 **Tylomyia** n. gen.

AGRIINI

SUBTRIBE WOHLFAHRTIINA

This subtribe consists of the genus *Wohlfahrtia* only. The abdomen has three rows of spots, Fig. 448. These spots may be confluent. The phallic tube is generally reduced. See Chart 3.

Genus *Wohlfahrtia* Brauer & Bergenstamm

Wohlfahrtia Brauer & Bergenstamm 1889. Denkschr. Akad. Wien 56: 123. Genotype *Sarcophila magnifica* Schin.

Agria Macquart 1835 (nec. R.-D.). Suites a Buffon, II, 229, 3. Genotype *Tachina nuba* Wied. (teste Séguy, 1941b).

Disjunctio Pandellé 1894. Rev. Entom. 13:56. Genotype *Sarcophaga tetripunctata* Dufour equals *W. bella* Macq.

Bracia Enderlein 1934. S. B. Ges. Naturf. Fr. Berlin, p. 189. Genotype *Tachina nuba* Wied.

Pandellea Enderlein 1934. S. B. Ges. Naturf. Fr. Berlin, p. 189. Genotype *Wohlfahrtia hungarica* B. & B. equals *W. meigeni* Schin.

Front protuberant; arista bare or with very short hairs; frontal row not divergent; notopleurals two; sternopleurals two; apicoscutellars absent; anterior acrosticals variable; 3 to 5 PSDC; not all equal in strength; hind tibiae may have a short fringe; abdomen with three rows of black spots; may be confluent in some cases; 5S with margin entire, Fig. 17; phallus with apex closed over; appearing hollowed out in some species, Figs. 18, 19; forms wide or narrow trough; corpus may have projections on either side; phallic tube reduced, Figs. 18, 19, or moderately conspicuous.

The species of the genus *Wohlfahrtia* are present in all regions except the Neotropical and Australian. The genus is primarily Palearctic. The species are noted for their myiasis production in man. Walker (1920 and 1922), Johannsen (1921 and 1926), Felt (1924), Ford (1936), and others have studied the biology of some of the species of *Wohlfahrtia*. According to Séguy (1941b), Rohdendorf has recorded *W. trina* (Wied.) as a parasite of *Schistocerca gregaria* Forsk. Séguy (1941a) treats many of the species of this genus and their biology. Potgieter (1929) records *W. euvittata* Vill. as an egg parasite of *Locustana*.

Included Species		
<i>atra</i> Aldrich 1926	P	D (Aldrich 1926)
<i>bella</i> (Macquart) 1836	P	D (Salem 1938a)
<i>brunnipalpis</i> (Macquart) 1850	P	D (Salem 1938a)
<i>erythrocer</i> a Villeneuve 1931	P,E	D (Salem 1938a)
<i>euvittata</i> Villeneuve 1920	E	D (Salem 1938a)
<i>indigens</i> Villeneuve 1928	P	D (Patton 1939)
<i>indigens aethiopica</i> Villeneuve 1928	E	D (Salem 1938a)
<i>intermedia</i> (Portchinsky) 1887	P	D (Salem 1938a)
<i>magnifica</i> (Schiner) 1862	P	D (Patton 1939)
<i>meigeni</i> (Schiner) 1862	Ne,P	D (Salem 1938a)
<i>nuba</i> (Wiedemann) 1830	P,O,E	D (Patton 1939)
<i>pattoni</i> Salem 1938a	P	D (Salem 1938a)
<i>seguyi</i> Salem 1938a	E	D (Séguy 1941b)
<i>smarti</i> Salem 1938a	E	D (Salem 1938a)
<i>trina</i> (Wiedemann) 1830	P,E	D (Patton 1939)
<i>triquetra</i> Séguy 1931	P	D (Séguy 1941b)
<i>vigil</i> (Walker) 1849	Ne	S
<i>villeneuvei</i> Salem 1938a	P	D (Salem 1938a)

SUBTRIBE SARCOFAHRTIINA

This subtribe contains the single genus *Sarcophahrtia*. The corpus is partially closed over ventrally, Figs. 14, 15, the phallic tube may be very long, Fig. 14, and the ventral sclerotization indistinct. Anal plate is distant from anal forceps, Fig. 449, may appear fused to ninth tergum.

Genus *Sarcophahrtia* Parker

Sarcophahrtia Parker 1916a. *Psyche* 23:131. Genotype *Sarcophahrtia ravinia* Park.

Thelodiscus Aldrich 1916. *Sarcophaga* and allies, p. 61. Genotype *Thelodiscus indivisus* Ald. equals *Sarcophahrtia ravinia* Park.

Frontal rows divergent over their entire length; outer verticals absent; 4+ post-ocular rows; 3 PSDC; anterior acrosticals absent; 2 notopleurals; scutellars 3-1-0; 2A with only laterals; 3A with MM; IV and hind tibiae bare; 5S as in Fig. 16; essential phallic characters given above.

All the species placed in this genus are North American. Their biology is unknown.

Included Species		
<i>atlantica</i> Parker 1919b	Ne	D (Parker 1919b)
<i>madisoni</i> Parker 1919b	Ne	D (Parker 1919b)
<i>montanensis</i> Parker 1919b	Ne	D (Parker 1919b)
<i>ravinia</i> Parker 1916a	Ne	S

SUBTRIBE AGRIINA

This subtribe consists of the single genus *Agria* R. D. The abdomen here is normally tessellated and the ventral sclerotization is greatly enlarged and developed. See Chart 3.

Genus *Agria* Robineau-Desvoidy

Agria Robineau-Desvoidy 1830. Ess. Myod., p. 376. Genotype *Musca affinis* Fall.

Pseudosarcophaga Kramer 1908b. Ent. Woch., 25:200. Genotype *Musca affinis* Fall. designation by Enderlein 1928a.

Frontal rows very gradually divergent over entire length; outer verticals absent; 3 or 4 post-ocular rows; 3 PSDC; anterior acrosticals present; 2 notopleurals; scutellars 3-1-0; 2A with laterals only; 3A with MM; 1V bare; hind tibiae bare; 5S with margin entire; corpus opens ventrally, with anterior projections, Figs. 11-13; ventral sclerotization greatly enlarged with long lateral dorsal projections, Fig. 13.

The taxonomy of this genus is in a slightly confused state at present. Aldrich (1916) and Senior-White (1940) credit the genus to Robineau-Desvoidy with *Musca affinis* Fallén as type. Townsend (1937) also credits the genus to Robineau-Desvoidy but gives *A. punctata* R. D. equals *Musca latifrons* Fallén as genotype. The genotype designation was by Townsend (1916). Séguy (1941b) credits the genus to Macquart (1835) with *Musca affinis* Fallén as type.

The type species is Nearctic and Palearctic in distribution. It has been reared from *Vanessa antiopa* (Aldrich 1916) and other insects. Séguy (1932a) lists it as a grasshopper parasite, and Thompson (1943-47) lists it as a parasite on Tenthredinidae and Lymantridae. Other species that have been placed here were not available for study, and the descriptions were not sufficiently clear to place them here.

SARCOPHAGINI

Series 1

This is the most primitive of the series of the Sarcophagini. The characters given under the only subtribe and genus (*Impariina* and *Imparia* n. gen.) will suffice to define the series. See Chart 3.

SUBTRIBE IMPARIINA

This is the most aberrant of all the subtribes of the Sarcophagini. The asymmetrical phallus is unique. Its primitive position, Chart 3, is due to the presence of a very large phallic tube. Such a tube is possessed by no other sarcophagid. Its external characters are not distinctive. It consists of only one genus.

Genus *Imparia* new genus

Frontal row divergent in last 2 bristles; outer vertical absent; 3 post-ocular rows; 4 or 5 PSDC, anterior 2 small; anterior acrosticals present; scutellars 2-1-1; 2A and 3A with laterals only; 1V and hind tibiae bare;

5S as in Fig. 23; phallus asymmetrical, Figs. 20-22; large phallic tube present; anal forceps very sharply hooked, Fig. 451.

Genotype and only species *Sarcophaga impar* Ald. by present designation.

The genotype is North American and has been recorded as a parasite and from beef refuse (Aldrich 1916) and has been reared from garbage by the author.

Series 2

This series is characterized by the tripartite split of the ventral sclerotization before it undergoes modification. It is more primitive than Series 3 in habits, containing many coprophagous and saprophagous genera and species. Many of its species are capable of developing either as scavengers or as true parasites. The subtribe Sarcophagulina and the *Johnsonia* group contain some of the most generalized of the Sarcophagini. The genera *Camptops* and *Sarcophagula* both contain species with 2 notopleurals, proclinate fronto-orbitals in the male and very generalized phalli.

There are five subtribes in this series. They are Sarcophagulina, Hypopeltina, Sarcophagina, Raviniina, and Hystricocnemina. See Chart 3 for the relationships of these subtribes.

SUBTRIBE HYPOPELTINA

This subtribe consists of the one genus *Hypopelta* Ald. Like *Imparia*, its phallus is unique among those of the Sarcophagini. The corpus is generally turned anteriorly, and is almost at right angles to the phallophore. The basally sclerotized section sends out two large plates which give the corpus a boat-like appearance. The dorsally projecting vesica is like a sail. It is probably an early offshoot of the sarcophagine-raviniine line, Chart 3, and is here given subtribal rank.

Genus *Hypopelta* Aldrich

Hypopelta Aldrich 1916. *Sarcophaga* and allies, p. 49. Genotype *Hypopelta scrofa* Ald.

Frontals diverging rapidly below; outer verticals present; 3 post-ocular rows; 3 PSDC; anterior acrosticals absent; scutellars 1-0-1, the apicals could be considered as laterals giving a 1-1-0 formula; 2A with only laterals; 3A with MM; abdomen large and clubbed apically; 5S with oval lobes on inner margins of sternal arms; posterior claspers black, tubular, turned outward; phallus as in Figs. 30-32.

The genotype, the only species, is North American. Its biology is not known.

SUBTRIBE SARCOPHAGULINA

This is one of the most primitive of the subtribes of Sarcophagini. The fifth sternite is very small and generalized and the lateral arms are still attached to the corpus and have not moved from their original position. The retention of proclinate fronto-orbitals in the male and 2 notopleural bristles also place this subtribe in a rather primitive position. It has been placed as an early offshoot of the sarcophagine-ravinine stock, Chart 3. It consists of only one genus, *Sarcophagula* Wulp.

Genus *Sarcophagula* Van der Wulp

Sarcophagula Van der Wulp 1887. Tijdsch. V. Ent., 30:173. Genotype *Musca occidua* Fab. designation by Coquillett 1910.

Sarothromyia Brauer & Bergenstamm 1891. Zweifl. Kais. Mus. V, part 2:365. Genotype *Sarcophila femoralis* Schin.

Frontal rows not divergent; 1 or 2 proclinate fronto-orbitals; outer verticals present; 4 or 5 post-ocular rows; 3 PSDC; anterior acrosticals absent; 2 notopleurals; scutellars 2-1-0; 2A and 3A with only laterals; 1V and hind tibiae bare; 5S small and weakly indented, Figs. 24, 28; corpus closed over ventrally; vesica well developed, Figs. 25, 27, 29; no juxta; ventral sclerotization forms median process and lateral arms, Fig. 26; very little modification.

The members of this genus are found in and around the Caribbean region: Cuba, Florida, Bahamas, Puerto Rico, Panama, and Jamaica. *S. femoralis* var. *simplex* (Ald.) has been reared from decaying fish (Hall 1932).

The above species are the only ones placed in the genus. Aldrich (1916) has described a variety *simplex* of *S. femoralis*. Other species have been placed here by other authors but the descriptions and figures do not support their placement in this genus.

SUBTRIBE SARCOPHAGINA

This is the largest of the subtribes of the tribe Sarcophagini. It is characterized by the median process being fused to the juxta and the well-developed lateral filaments. The species run the gamut of nutrition from coprophagous and saprophagous to true parasitism. It consists of two generic groups, the *Sarcophaga* and *Johnsonia* groups. See Charts 3, 4, and 5 for the evolution of the groups, genera and species.

Johnsonia Group

This group is characterized by the presence of the reduced phallic tube, Fig. 46, or lateral plates, Fig. 44, or a highly membranous phallus, Fig. 36. The vesica is generally lacking. Both notopleurals and PSDC

run from 2 to 4. The capitis is present only in the genus *Helicobia*. The fifth sternite may be small. The group consists of the genera *Camptops*, *Chloronesia*, *Argoravinia*, *Johnsonia*, and *Helicobia*. See Chart 4 for the evolution of its genera and species.

Genus *Camptops* Aldrich

Camptops Aldrich 1916. *Sarcophaga* and Allies, p. 34. Genotype *Camptops unicolor* Ald.

Harpagopyga Aldrich 1916. *Sarcophaga* and allies, p. 61. Genotype *Sarcophaga diversipes* Coq.

Frontal rows not divergent below; outer verticals present; oral vibrissae may be above the oral margin; 3 post-ocular rows; anterior acrosticals absent; 3 to 6 hypopleurals; scutellars 3-0-0; 2 notopleurals; 2A with only laterals or a row; 3A with marginal row of bristles; 1V bare or setulose; hind tibiae bare; 4S small, moderately indented, Fig. 35; corpus mostly membranous, Fig. 36; vesica membranous, Figs. 34, 36; juxta, lateral filaments, and fused median process present.

The genitalia of the two genera listed above are very similar, if not almost identical. On the basis of this and the general similarity in chaetotaxy the types are considered to be congeneric.

The species of this genus are New World in distribution. Thompson (1947) lists *H. diversipes* as a parasite of *Laphygma* (Phalaenidae).

Included Species

<i>angustiventris</i> (Curran & Walley) 1934	No	D (Curran & Walley 1934)
<i>divergens</i> (Curran & Walley) 1934	No	D (Curran & Walley 1934)
<i>diversipes</i> (Coquillett) 1900	No	D (Aldrich 1916)
<i>unicolor</i> Aldrich 1916	No	S

Genus *Chloronesia* Townsend

Chloronesia Townsend 1912a. Proc. U. S. Nat. Mus. 43:360. Genotype *Chloronesia andina* Tns. (♀)

Notochaeta Aldrich 1916. *Sarcophaga* and allies, p. 52. Genotype *Notochaeta subpolita* Ald. equals *Sarcophaga fuscianalis* Wulp.

Micronotochaeta Townsend 1927. Rev. Mus. Paulista 15:233. Genotype *Micronotochaeta costalis* Tns. teste Lopes 1946b.

Udamoctis Enderlein 1928a. Klass. Sarc., p. 25. Genotype *Udamoctis bogatana* End. teste Lopes 1946b.

Frontal row partly divergent in last 2 bristles; facialia ciliated up to more than halfway to antennal bases; 2 or 3 post-ocular rows; outer vertical rarely well differentiated; 2 or 3 PSDC; 2 to 4 notopleurals; anterior acrosticals variable, generally not well differentiated; propleura generally pilose; scutellars absent; prosternum pilose; 2A with laterals; 3A with

MM to a row; hind tibiae bare; IV bare; 4S as in Fig. 42; phallus largely membranous; fused median process and the lateral filaments present, Fig. 41; distinct vesica not present; trace of phallic tube present.

The genera *Chloronesia* Tns. and *Notochaeta* Ald. have been separated on the basis of the facialia being ciliate more than half way from the vibrissae to the base of the antennae and the arista plumose almost to the apex in *Chloronesia*, these conditions not being present in *Notochaeta*. The author has examined a male *Chloronesia* sent to him by Dr. Dodge and has found that genitallically it is not separable from *Notochaeta*. The characters given above are not considered sufficient for generic distinction.

The genus is almost entirely Mexican and tropical New World in distribution. *C. aldrichi* (Lopes) and *C. confusa* (Lopes) have been reared from Oligochaeta, Lopes (1942 & 1946b).

Included Species

<i>aldrichi</i> (Lopes) 1942	No	D (Lopes 1942)
<i>angusta</i> (Aldrich) 1925	No	D (Lopes 1946b)
<i>bogotana</i> (Enderlein) 1928a	No	D (Lopes 1946b)
<i>comata</i> (Aldrich) 1925	No	D (Lopes 1946b)
<i>confusa</i> (Lopes) 1946b	No	D (Lopes 1946b)
<i>costalis</i> (Townsend) 1927	No	D (Lopes 1946b)
<i>cyaniventris</i> (Lopes) 1946b	No	D (Lopes 1946b)
<i>dimidiata</i> (Wiedemann) 1830	No	D (Lopes 1946b)
<i>distincta</i> (Lopes) 1947a	No	D (Lopes 1947a)
<i>diversa</i> (Lopes) 1946b	No	D (Lopes 1946b)
<i>diversinervis</i> (Van der Wulp)	Ne	D (Lopes 1946b)
1896		
<i>fumipennis</i> (Lopes) 1946b	No	D (Lopes 1946b)
<i>fuscianalis</i> (Van der Wulp) 1896	Ne, No	D (Lopes 1946b)
<i>ignota</i> (Lopes) 1947a	No	D (Lopes 1947a)
<i>micropyga</i> (Van der Wulp) 1896	Ne	D (Lopes 1946b)
<i>obscura</i> (Lopes) 1950a	No	D (Lopes 1950a)
<i>parva</i> (Lopes) 1946b	No	D (Lopes 1946b)
<i>plumigera</i> (Van der Wulp) 1896	Ne	D (Lopes 1946b)
<i>rustica</i> (Lopes) 1950a	No	D (Lopes 1950a)
<i>sp.</i>	No	S
<i>townsendi</i> (Aldrich) 1925	No	D (Lopes 1946b)
<i>uniseta</i> (Lopes) 1950a	No	D (Lopes 1950a)
<i>viridis</i> (Lopes) 1950a	No	D (Lopes 1950a)

Genus *Argoravinia* Townsend

Argoravinia Townsend 1917b. Proc. Biol. Soc. Wash. 30:190. Genotype *Sarcophaga argentea* Tns. equals *Sarcophaga fissa* Ald. equals *Sarcophaga modesta* Wied. teste Ald. 1930.

Frontal row barely divergent; outer verticals present; 2 post-ocular rows; 4 PSDC, 2 small, 2 large; anterior acrosticals not distinct; scutellars 2-1-0; 2A with laterals only; 3A with MM; IV setulose, hind tibiae bare;

5S with long base and no window, Fig. 37; median process very long and sinuate, Fig. 39; vesica small; lateral filaments Y-shaped; no juxta.

The only species considered here, the type species, is recorded from Panama, the West Indies, and South America. The biology is not known.

Genus *Johnsonia* Coquillet

Frontal row divergent in last 1 to 3 bristles; outer vertical absent; 3 or 4 post-ocular rows; 3 or 4 PSDC; anterior acrosticals poorly differentiated; scutellar bristles variable; 1V bare or setose; 5V bare or setose; hind tibiae bare; 2A with MM present or absent; 3A with or without MM; reduced phallic tube present; lateral filaments and median process fused to juxta present; lateral plates small; vesica present or absent; Figs. 43-51.

Key to Subgenera—Males

1. First vein bare; vesica present; posterior dorsocentrals, 4 in number **Emblemasoma**
First vein setulose; vesica absent; posterior dorsocentrals, 3 in number **Johnsonia**

Subgenus *Emblemasoma* Aldrich

Emblemasoma Aldrich 1916. *Sarcophaga* and allies, p. 56. Genotype *Emblemasoma* *erro* Ald.

The characters given in the key are sufficient to define the subgenus; see Figs. 45 to 47 for the genitalia.

The species of this subgenus are New World in distribution. The biology is not known.

Included Species

<i>erro</i> (Aldrich) 1916	Ne, No	S
<i>faciale</i> (Aldrich) 1916	Ne	D (Aldrich 1915)

Subgenus *Johnsonia* Coquillet

Johnsonia Coquillet 1895. Proc. Acad. Nat. Sci. 47:316. Genotype *Johnsonia elegans* Coq.

Sthenopyga Aldrich 1916. *Sarcophaga* and allies, p. 59. Genotype *Sthenopyga globosa* Ald. equals *Sarcophaga rufitibia* Wulp.

5V bare or setose; otherwise key characters will suffice to define the subgenus. See Figs. 43, 44, 48-51.

The members of this subgenus are New World in distribution. Their biology is not known.

Included Species

<i>bivittata</i> Curran 1928	No	D (Curran 1928)
<i>borealis</i> Reinhard 1937	Ne	D (Hallock 1939)
<i>elegans</i> Coquillet 1895	Ne	D (Aldrich 1916)
<i>frontalis</i> Aldrich 1929	Ne	D (Aldrich 1929)
<i>lagunicula</i> Hall 1933a	No	D (Hall 1933a)

<i>rufitibia</i> (Van der Wulp) 1896	Ne	S
<i>setosa</i> Aldrich 1916	No	D (Aldrich 1916)
<i>sp.</i>	Ne	S

Genus **Helicobia** Coquillet

Helicobia Coquillet 1895. Proc. Acad. Nat. Sci. Phil. 317. Genotype

Helicobia heliciis Tns. equals *Sarcophaga rapax* Walk.

Helicobiopsis Townsend 1927. Rev. Mus. Paulista 12:313. Genotype

Helicobiopsis aurescens Tns. teste Lopes 1938c.

Notochaetophyto Hall 1933a. Bull. Amer. Mus. Nat. Hist. 46:258. Genotype *Notochaetophyto resinata* Hall teste Lopes 1938c.

Frontal row barely divergent; outer vertical variable; 3 post-ocular rows; 3 PSDC; anterior acrosticals seldom well developed; scutellars 2-1-1; 2A with laterals only; 3A with MM; 1V setulose; hind tibiae bare; 5S with window and moderate base, Figs. 53, 60; vesica absent; lateral plates present (except *H. australis* J. & T.), Figs. 58, 62; juxta depressed, with fused median process; capitis present, Figs. 54, 59; lateral filaments present, Figs. 56, 59.

The members of this genus are New World. The species placed in *Helicobia* Coq. by Curran (1934a) do not, if the published figures can be relied on, belong in *Helicobia* Coq. as constituted here. *H. australis* J. & T. is tentatively included here, but it is believed that it will fall in a separate genus when more of the Australian and Oriental fauna has been critically examined.

H. rapax will develop as a scavenger, Hayes (1917), Graenicher (1931), and as a parasite of various insects, Aldrich (1916), Plank (1929), Decker (1931), Breakey (1931), Thompson (1943-47), and others. Fuller (1938) has worked out the biology of *H. australis*. Thompson (1947) records *H. surrubea* as a parasite of *Diatrea*.

Included Species

<i>aurescens</i> (Townsend) 1927	No	D (Lopes 1938c)
<i>australis</i> Johnston & Tiegs 1921	A	S
<i>borgmeeri</i> Lopes 1938c	No	D (Lopes 1938c)
<i>iheringi</i> Lopes 1938c	No	D (Lopes 1938c)
<i>morionella</i> (Aldrich) 1930	Ne, No	S
<i>neglecta</i> Lopes 1946a	Ne	D (Lopes 1946a)
<i>pilifera</i> Lopes 1938c	No	D (Lopes 1938c)
<i>piliplaura</i> Lopes 1938c	No	T (Lopes 1938c)
<i>rapax</i> (Walker) 1849	Ne, No	S
<i>resinata</i> (Hall) 1933a	No	T (Lopes 1938c)
<i>setinervis</i> Lopes 1938c	No	D (Lopes 1938c)
<i>stellata</i> (Van der Wulp) 1896	Ne	S (Lopes 1947b)
<i>surrubea</i> (Van der Wulp) 1896	Ne	D (Lopes 1938c)

Sarcophaga Group

This group is characterized by the lack of a phallic tube and lateral

plates; a vesica is generally present as is the capitis on the fused median process. The fifth sternite is well developed and there are never less than 4 notopleurals (not all equally developed) and 3 PSDC. It consists of the genera *Sarcomyia* n. gen., *Sapromyia* n. gen., *Wohlfahrtiopsis*, *Arachnidomyia*, and *Sarcophaga*. See Chart 5 for the evolution of its genera and species.

Genus *Sarcomyia* new genus

Frontal row divergent in last 2 bristles; outer verticals present; 4 post-ocular rows; 4 PSDC; anterior acrosticals weak; scutellars 2-1-0 or 1; 2A with laterals only or weak MM; 3A with MM; 1V and hind tibiae bare; corpus and juxta continuous forming a claw-shaped structure, Fig. 79; vesica bent vertically at its middle, Fig. 79; 5S as in Fig. 81.

Genotype *Sarcophaga scelestus* Hall by present designation.

Included Species

<i>scelestus</i> (Hall) 1931b	Ne, No	S
<i>scelestus adunca</i> (Hall) 1933a	No	D (Hall 1933a)

Genus *Wohlfahrtiopsis* Townsend

Wohlfahrtiopsis Townsend 1917a. Proc. Biol. Soc. Wash. 30:45. Genotype *Sarcophaga johnsoni* Ald.

Scarabaeophaga Townsend 1918. Ins. Ins. Mens. V:160. Genotype *Sarcophaga utilis* Ald.

Petrosarcophaga Townsend 1919. Proc. U. S. Nat. Mus., 56:543. Genotype *Petrosarcophaga arizonica* Tns. equals *Sarcophaga bishoppi* Ald.

Frontal row rapidly divergent below; outer verticals present or absent; post-ocular rows 2 or 3; PSDC 5, generally 3 weak 2 strong; anterior acrosticals absent; scutellars 2-1-1; 2A with laterals only; 3A with MM; 1V bare; hind tibiae bare except a few short hairs in *W. johnsoni* (Ald.); 5S with long base, no window; a few strong bristles on inner edges of sternal arms near base of V; corpus unusually shaped, Figs. 82, 86, 89; vesica large and bizarre; juxta free; capitis long and almost detached; Fig. 87. Yellow mass often surrounds phallus.

The three genotypes listed above are the only species in this genus. They are all North American. *W. utilis* (Ald.) has been reared from *Geotrupes splendens* and *Allorhina nitida*, Aldrich (1916), and *Phyllophaga*, Davis (1919). The biology of the others is not known.

Genus *Sapromyia* new genus

Frontal row moderately divergent; outer verticals absent; 2 or 3 post-ocular rows; 5 PSDC, 3 weak 2 strong; anterior acrosticals absent; scutellars 2-1-1; 2A with laterals only; 3A with MM, except *S. cooleyi* (Park.); 1V bare; hind tibiae villous; 5S with long base, no window, brush of

bristles on each arm near base of V, Figs. 91, 95, 101; vesica is 2 ventrally setose lobes, Fig. 97; juxta free; capitis small and membranous, Figs. 92, 98, 102, genitalia, Figs. 90-102.

Genotype: *Sarcophaga bullata* Park. by present designation.

The species of this group are mostly North American. Only *S. polistensis offecta* (Lopes) is recorded from South America. *S. cooleyi* (Park.) has been reported from decaying garbage, particularly fish, Aldrich (1916). Twinn (1934) and Stewart (1934) have reported on a case of auricular myiasis involving *S. cooleyi*. Graenicher (1931) has reared *bullata* from decaying meat and insects and (1935) from human excrement. James (1947) mentions *S. bullata* as being incriminated in intestinal myiasis. The author has reared *S. bullata* (Park.) from garbage. *S. polistensis* has been reared from wasps' nests, Hall (1933b). The biology of the others is not known.

Included Species

<i>bullata</i> (Parker) 1916c	Ne	S
<i>cooleyi</i> (Parker) 1914a	Ne	S
<i>libera</i> (Aldrich) 1916	Ne	D (Aldrich 1916)
<i>polistensis</i> (Hall) 1933b	Ne	S
<i>polistensis offecta</i> (Lopes) 1938b	No	D (Lopes 1938b)

Genus *Arachnidomyia* Townsend

Arachnidomyia Townsend 1934a. Rev. Ent. Rio de Janeiro 4:111. Genotype *Sarcophaga davidsoni* Coq.

Frontals divergent in last 2 or 3 bristles; outer verticals present or absent; 3 post-ocular rows; 3-5 PSDC; anterior acrosticals variable; scutellars 2-1-1; 2A with or without MM; 3A with MM; IV bare; hind tibiae bare; 5S well developed, with window, Fig. 65; juxta broad and short; broadly attached to corpus, Figs. 68, 72; median process forward on juxta, Figs. 69, 70, 73; capitis mostly sclerous; harpes and vesica not well developed; lateral filaments may be expanded distally with slight apical spur, Figs. 68, 74.

This genus ranges from U. S. to Cuba. *A. davidsoni* (Coq.) and *A. subaenescens* (Ald.) have been recorded as spider egg mass parasites, Aldrich (1916 & 1925). *A. houghi* (Ald.) is parasitic on Lepidoptera, Knull (1932), Glendenning (1914). *A. aldrichi* (Park.) has been reared from Lepidoptera, Parker (1916), and Glendenning (1914).

Included Species

<i>aldrichi</i> (Parker) 1916d	Ne	S
<i>davidsoni</i> (Coquillett) 1892	Ne, No	S
<i>hinei</i> (Aldrich) 1916	Ne	S
<i>houghi</i> (Aldrich) 1916	Ne	S
<i>subaenescens</i> (Aldrich) 1925	Ne	D (Aldrich 1925)

Genus *Sarcophaga* Meigen

- Sarcophaga** Meigen 1826. Syst. Bes. V, 14. Genotype *Musca carnaria* Linn. Designation by Westwood 1840.
- Myophora** Robineau-Desvoidy 1830. Ess. Myod. 337. Genotype *Musca carnaria* Linn.
- Pierretia** Robineau-Desvoidy 1863. Hist. Dipt. II 422. Genotype *Pierretia praecox* R. D. designation by Townsend 1917, equals *Sarcophaga nigriventris* Meig.
- Bellieria** Robineau-Desvoidy 1863. Hist. Dipt. II 432. Genotype *Myophora cinerea* R. D. equals *Sarcophaga melanura* Meig. teste Townsend 1938.
- Scaligeria** Robineau-Desvoidy 1863. Hist. Dipt. II 478. Genotype *Myophora maialis* R. D. equals *Myophora cinerea* R. D. teste Townsend 1938.
- Erichsonia** Robineau-Desvoidy 1863 (Preocc.) Hist. Dipt. II 481. equals *Mulsantia* teste Townsend 1938. Genotype *Sarcophaga haemorrhoea* Meig.
- Hartigia** Robineau-Desvoidy 1863. Hist. Dipt. II 521. Genotype *Hartigia concolor* R. D. equals *Sarcophaga dissimilis* Meig. teste Townsend 1938.
- Bercaea** Robineau-Desvoidy 1863. Hist. Dipt. II 549. Genotype *Bercaea haemorrhoidalis* R. D. equals *Musca haemorrhoidalis* Fallén.
- Mulsantia** Robineau-Desvoidy 1863. Hist. Dipt. II 557. Genotype *Mulsantia campestris* R. D. Designation by Coquillett 1910, equals *Sarcophaga haemorrhoea* Meigen, teste Townsend 1938.
- Calypitia** Robineau-Desvoidy 1863. Hist. Dipt. II 576. Genotype *Calypitia carceli* R. D. Designation by Townsend 1916, equals *Myophora cinerea* R. D. teste Townsend 1938.
- Heteronychia** Brauer & Bergenstamm, 1889. Zweifl. Kais. Mus. IV part I; 124. Genotype *Heteronychia chaetonura* B. & B. Congeneric with *Hartigia concolor* R. D. teste Townsend 1938.
- Sarcotachinella** Townsend 1892a. Tr. Am. Ent. Soc. XIX, 110. Genotype *Sarcotachinella intermedia* Tns. equals *Sarcophaga sinuata* Meig.
- Bercaeopsis** Townsend 1917b. Proc. Biol. Soc. Wash. 30:192. Genotype *Sarcophaga tetra* Ald.
- Sarracenyia** Townsend 1917b. Proc. Biol. Soc. Wash. 30:192. Genotype *Sarcophaga sarraceniae* Riley.
- Parasarcophaga** Johnston & Tiesg 1921. Proc. Roy. Soc. Queensland 23:78. Genotype *Sarcophaga omega* J. & T.
- Robinauella** Enderlein 1928a. Klass. Sarc.:29. Genotype *Sarcophaga scoparia* Pandellé.
- Mehria** Enderlein 1928a. Klass. Sarc.:29. Genotype *Sarcophaga nemoralis* Kramer.

- Discachaeta** Enderlein 1928a. Klass. Sarc.:30. Genotype *Sarcophaga cucullans* Pandellé.
- Arhopocnemis** Enderlein 1928a. Klass. Sarc.:33, equals *Sarcotachinella* Townsend. Genotype *Sarcophaga sinuata* Meigen.
- Athysia** Enderlein 1928a. Klass. Sarc.:34, equals *Pierretia* R. D. teste Townsend 1938. Genotype *Sarcophaga nigriventris* Meigen.
- Villeneuveella** Enderlein 1928a. Klass. Sarc.:34. Genotype *Sarcophaga soror* Rond.
- Helicophagella** Enderlein 1928a. Klass. Sarc.:38. Genotype *Sarcophaga noverca* Rond.
- Ctenodasyphygia** Enderlein 1928a. Klass. Sarc.:40. Genotype *Sarcophaga fertoni* Vill.
- Dasyphygia** Enderlein 1928a. Klass. Sarc.:40. Genotype *Sarcophaga arvorum* Rond. nec Meig. equals *Sarcophaga depressifrons* Zett.
- Liopygia** Enderlein 1928a. Klass. Sarc.:41. Genotype *Musca ruficornis* Fabr.
- Thyrsochnema** Enderlein 1928a. Klass. Sarc.:42. Genotype *Sarcophaga incisilobata* Pandellé.
- Kramerella** Enderlein 1928a. Klass. Sarc.:48, equals *Hartigia* R. D. teste Townsend 1937. Genotype *Sarcophaga granulata* Kramer.
- Sarina** Enderlein 1928a. Klass. Sarc.:48. Genotype *Sarcophaga nigrans* Pand. equals *Sarcophaga clathrata* Meig.
- Boettcherella** Enderlein 1928a. Klass. Sarc.:49. Genotype *Sarcophaga setinervis* Rond.
- Athysomima** Rohdendorf 1937. Faune d'U.R.S.S.:185. Genotype *Athysomima stackelbergi* Rohdendorf.
- Pandelleana** Rohdendorf 1937. Faune d'U.R.S.S.:189. Genotype *Sarcophaga protuberans* Pandellé.
- Stackelbergeola** Rohdendorf 1937. Faune d'U.R.S.S.:257. Genotype *Sarcophaga mehadiensis* Böttcher.
- Phallocheira** Rohdendorf 1937. Faune d'U.R.S.S.:267. Genotype *Phallocheira minor* Rohdendorf.
- Boettcherisca** Rohdendorf 1937. Faune d'U.R.S.S.:270. Genotype *Sarcophaga peregrina* R. D.
- Kramerea** Rohdendorf 1937. Faune d'U.R.S.S.:274. Genotype *Sarcophaga schutzei* Kram.
- Harpagophalla** Rohdendorf 1937. Faune d'U.R.S.S.:276. Genotype *Sarcophaga sera* Rohdendorf.
- Hoa** Rohdendorf 1937. Faune d'U.R.S.S.:291. Genotype *Sarcophaga flexuosa* Ho.
- Coprosarcophaga** Rohdendorf 1937. Faune d'U.R.S.S.:293. Genotype *Sarcophaga haemorrhoidalis* Fall.

Phytosarcophaga Rohdendorf 1937. Faune d'U.R.S.S.:301. Genotype *Sarcophaga destructor* Malloch.

Tricholioproctia Baranoff 1938. Bull. Ent. Res. 29:414. Genotype *Sarcophaga antilope* Bött.

Probellieria Blanchard 1942. Physis, 19:149. Genotype *Sarcophaga barbata* Thoms. equals *Sarcophaga argyrostoma* R. D.

This genus as considered here is the largest and most widespread of all sarcophagine genera. It has been divided into many small genera by various authors in different parts of the world, hence the rather ponderous synonymy above. It is felt, that, for the present, the relationship of the species included is best expressed by considering *Sarcophaga*, in the sense used here, as a single large genus. The genera proposed by Rohdendorf (1937) if lowered to subgeneric rank are the best subdivisions of this genus as yet proposed. A study of the entire world fauna will be necessary to solve the problem fully. Most of the new species described by Rohdendorf (1937), from page 129 on, will fall in *Sarcophaga* as considered here. The genus *Stephanostoma* Lenz, as proposed by Townsend (1938), is not accepted here.

Frontal row divergent in last 2-5 bristles; ocellars well developed; 3 or 4 post-ocular rows; outer verticals present or absent; 3-6 PSDC; if more than 4, not equal in thickness; scutellars 2 or 3-1-1; apical may be absent; 3-12 hypopleurals; 2A occasionally with MM; 3A with MM to a complete row; hind tibiae generally villous; IV bare; 5S, Figs. 116, 142, 200, large and well developed; vesica, juxta, median process fused to juxta and lateral filaments, Figs. 102, 133, 160, present; harpes and capitis generally present; phallopore and phallus always separate. Genitalia in Figs. 33-214.

The distribution is almost world-wide. *Sarcophaga* is found in all regions but is very poorly represented in the neotropical. Its presence in the oceanic islands in the Pacific is undoubtedly due to introduction.

The genus *Sarcophaga* is very large and its food habits run the gamut from saprophagous and coprophagous nutrition to human parasitism. This is often true of a single species such as *S. haemorrhoidalis*. It has been reared from dung, Aldrich (1916), Knipling (1936); has been reported as a parasite of insects, Hinds & Dew (1915), Regnier (1931), Webster (1907); and has been incriminated in cases of human intestinal myiasis, Aldrich (1916), Haseman (1917). *S. sarraceniae* has been reared from *Sarracenia*, Aldrich (1916); and Thompson (1943) recorded it as a parasite of *Allorhina nitida*. Members of this genus have been recorded as reared from dead insects, Jack (1935), decaying snails, decaying vegetable matter, dead toads and snakes, dead mammals, and parasitic on a lumbricid worm, Senior-White (1940). Séguy (1929) lists *S. melanura* reared from a swallow.

Included Species

<i>acadiana</i> Reinhard 1947	Ne	D (Reinhard 1947)
<i>aegyptica</i> Salem 1935	P	D (Salem 1935)
<i>albiceps</i> Meigen 1826	P,O,A	D (Séguy 1941b)
<i>alpha</i> Johnston & Tiegs 1921	A	D (Johnston & Hardy 1923)
<i>amita</i> Rondani 1861b	P	D (Séguy 1941b)
<i>ancilla</i> Rondani 1865	P	T (Séguy 1941b)
<i>ancilloides</i> Baranoff 1927	P	T (Baranoff 1927)
<i>antelope</i> Böttcher 1913c	O	D (S.-White et al. 1940)
<i>aratrix</i> Pandellé 1896	P	S
<i>arcipes</i> Pandellé 1896	P	S
<i>argyrostoma</i> Robineau-Desvoidy 1830	Ne,No,P,O, E,Oc	S
<i>aurifrons</i> Macquart 1846	A	D (Johnston & Hardy 1923)
<i>ballardi</i> Senior-White 1924	O	T (S.-White et al. 1940)
<i>balmstadi</i> Curran 1934a	E	T (Curran 1934a)
<i>bancrofti</i> Johnston & Tiegs 1921	A	T (Johnston & Hardy 1923)
<i>banksi</i> Senior-White 1924	O	T (S.-White et al. 1940)
<i>basalis</i> Walker 1859	O	T (S.-White et al. 1940)
<i>beesoni</i> Senior-White 1924	O	T (S.-White et al. 1940)
<i>benaci</i> Böttcher 1913a	P	T (Séguy 1941b)
<i>beta</i> Johnston & Tiegs 1921	A	D (Johnston & Hardy 1923)
<i>bezziana</i> Böttcher 1913a	P	T (Séguy 1941b)
<i>bolivari</i> Gil Collado 1930	P	T (Séguy 1941b)
<i>böttcheriana</i> Rohdendorf 1937	P	D (Séguy 1941b)
<i>brevicornis</i> Ho 1934b	O	D (S.-White et al. 1940)
<i>burungae</i> Curran 1934a	E	T (Curran 1934a)
<i>carnaria</i> (Linnaeus) 1758	No,P	S
<i>caudegalli</i> Böttcher 1912c	O	T (S.-White et al. 1940)
<i>cessator</i> Aldrich 1916	Ne	T (Aldrich 1916)
<i>chaetonura</i> (Brauer & Bergenstamm) 1889	P	T (Séguy 1941b)
<i>clathrata</i> Meigen 1826	P	T (Séguy 1941b)
<i>cockerellae</i> Aldrich 1916	Ne	T (Aldrich 1916)
<i>concreata</i> Séguy 1935	O	D (Séguy 1941b)
<i>consanguinea</i> Rondani 1861b	P	D (Séguy 1941b)
<i>corsicana</i> Villeneuve 1911b	P	D (Séguy 1941b)
<i>crassipalpis</i> Macquart 1838	Ne,No,P,O,Oc	S
<i>cucullans</i> Pandellé 1896	P	S
<i>cultellata</i> Pandellé 1896	P	T (Séguy 1941b)
<i>czernyi</i> Böttcher 1912d	P	T (Séguy 1941b)
<i>demeillon</i> Zumpt 1950b	E	T (Zumpt 1950b)
<i>depressa</i> Robineau-Desvoidy 1830	A	D (Johnston & Hardy 1923)
<i>depressifrons</i> Zetterstedt 1845	P	D (Séguy 1941b)
<i>desertorum</i> Salem 1935	P	T (Salem 1935)
<i>destructor</i> Malloch 1929	P,E	T (Salem 1935)
<i>discifera</i> Pandellé 1896	P	D (Séguy 1941b)
<i>dissimilis</i> Meigen 1826	P	T (Séguy 1941b)
<i>dolescalli</i> Johnston & Tiegs 1921	A	D (S.-White et al. 1940)
<i>dura</i> Curran 1934a	E	D (Curran 1934a)
<i>elongata</i> Aldrich 1916	Ne	D (Aldrich 1916)
<i>epsilon</i> Johnston & Tiegs 1922b	A	D (Johnston & Hardy 1923)

<i>eta</i> Johnston & Tiegs 1921	A	D (Johnston & Hardy 1923)
<i>exuberans</i> Pandellé 1896	Ne,P	S
<i>falciforceps</i> Villeneuve 1929	E	T (Curran 1934a)
<i>ferox</i> Villeneuve 1908	P	T (Séguy 1941b)
<i>fertoni</i> Villeneuve 1911b	P	T (Séguy 1941b)
<i>flexuosa</i> Ho 1934a	P	T (Rohdendorf 1937)
<i>fortisa</i> Reinhard 1947	Ne	T (Reinhard 1947)
<i>frogatti</i> Taylor 1917	A	T (Johnston & Hardy 1923)
<i>fulvipes</i> Macquart 1842	Ne,No	S
<i>garbo</i> Curran 1934a	E	D (Curran 1934a)
<i>gnu</i> Curran 1934a	E	T (Curran 1934a)
<i>gracilis</i> Aldrich 1916	Ne	S
<i>granulata</i> Kramer 1908a	P	D (Séguy 1941b)
<i>guillermodi</i> Zumpt 1950a	E	D (Zumpt 1950a)
<i>haemorrhoea</i> Meigen 1826	P	S
<i>haemorrhoidalis</i> Fallén 1818	Ne,P,O,E,Oc	S
<i>haemorrhoides</i> Böttcher 1913a	P	D (Séguy 1941b)
<i>hardyi</i> Johnston & Tiegs 1922b	A	T (Johnston & Hardy 1923)
<i>harpax</i> Pandellé 1896	Ne,P,O,E,Oc	S
<i>henryi</i> Senior-White 1924	O	D (S.-White et al. 1940)
<i>hirticrus</i> Pandellé 1896	P	T (Séguy 1941b)
<i>hirtipes</i> Wiedemann 1830	Ne,P,O,E	D (Séguy 1941b)
<i>hollandia</i> Roback 1952	A	S
<i>hui</i> Ho 1936	O	D (S.-White et al. 1940)
<i>idmais</i> Séguy 1934	O	D (S.-White et al. 1940)
<i>idonea</i> Aldrich 1916	Ne	S
<i>imitatrix</i> Baranoff 1938	A	D (Baranoff 1938)
<i>incisilobata</i> Pandellé 1896	P	S
<i>infixa</i> Böttcher 1913a	P	T (Séguy 1941b)
<i>inzi</i> Curran 1934a	E	D (Curran 1934a)
<i>impatiens</i> Walker 1849	A	T (Hardy 1943)
<i>josephi</i> Böttcher 1912c	O	T (S.-White et al. 1940)
<i>juliaetta</i> Aldrich 1916	Ne	S
<i>kappa</i> Johnston & Tiegs 1921	A	D (Johnston & Hardy 1923)
<i>kawayuensis</i> Kano 1950	P	D (Kano 1950)
<i>kentejana</i> (Rohdendorf) 1937	P	D (Rohdendorf 1937)
<i>kentejana lapponica</i> Tiensuu 1939	P	D (Tiensuu 1939)
<i>kerteszi</i> Villeneuve 1912c	P	T (Séguy 1941b)
<i>khasiensis</i> Senior-White 1924	O	T (S.-White et al. 1940)
<i>kohla</i> Johnston & Tiegs 1921	A	C (Johnston & Hardy 1923)
<i>littoralis</i> Johnston & Tiegs 1922b	A	T (Johnston & Hardy 1923)
<i>longicornis</i> Macquart 1843	P	T (Séguy 1941b)
<i>lunigera</i> Böttcher 1914	P	T (Séguy 1941b)
<i>maculata</i> Meigen 1838	P	D (Séguy 1941b)
<i>marshalli</i> Parker 1923	P	D (Séguy 1941b)
<i>mehadiensis</i> Böttcher 1912b	P	D (Séguy 1941b)
<i>melanura</i> Meigen 1826	Ne,P,O	S
<i>mendax</i> Reinhard 1947	Ne	D (Reinhard 1947)
<i>mimoris</i> Reinhard 1947	Ne	T (Reinhard 1947)
<i>minor</i> (Rohdendorf) 1937	P	T (Rohdendorf 1937)
<i>minutissima</i> Hall 1929b	Ne	D (Hall 1929b)

<i>misera</i> Walker 1849	P,O,A	S
<i>montanensis</i> Hallock 1938	Ne	D (Hallock 1940)
<i>mulaba</i> Curran 1934a	E	T (Curran 1934a)
<i>musitali</i> Curran 1934a	E	D (Curran 1934a)
<i>musprattianus</i> Zumpt 1951	E	T (Zumpt 1951)
<i>natalensis</i> Zumpt 1951	E	D (Zumpt 1951)
<i>memoralis</i> Kramer 1908a	P	D (Séguy 1941b)
<i>nigriventris</i> Meigen 1826	P,O	S
<i>noverca</i> Rondani 1861b	P	T (Séguy 1941b)
<i>occidentalis</i> Aldrich 1916	Ne	S
<i>offuscata</i> Schiner 1862	P	S
<i>omega</i> Johnston & Tiegs 1921	A	D (Johnston & Hardy 1923)
<i>omikron</i> Johnston & Tiegs 1921	A	D (Johnston & Hardy 1923)
<i>orchidea</i> Böttcher 1913c	P,O,A	D (S.-White et al. 1940)
<i>ostindicae</i> Senior-White	O	T (S.-White et al. 1940)
<i>parallela</i> Aldrich 1916	Ne	S
<i>pattoni</i> Senior-White 1924	O	T (S.-White et al. 1940)
<i>pandellei</i> Rohdendorf 1937	P	D (Séguy 1941b)
<i>pauciseta</i> Pandellé 1896	P	T (Séguy 1941b)
<i>penicillata</i> Villeneuve 1907	P	D (Séguy 1941b)
<i>peregrina</i> Robineau-Desvoidy 1830	O,A,Oc	D (Séguy 1941b)
<i>perspicax</i> Aldrich 1916	Ne	D (Aldrich 1916)
<i>piva</i> Roback 1952	A	S
<i>preussi</i> Zumpt 1951	E	T (Zumpt 1951)
<i>privigna</i> Rondani 1861b	P	S
<i>procax</i> Séguy 1932	P	T (Séguy 1941b)
<i>prosbalina</i> Baranoff 1931	O	T (S.-White et al. 1940)
<i>protuberans</i> Pandellé 1896	P	S
<i>proxima</i> Rondani 1861b	P	T (Séguy 1941b)
<i>pseudoscoparia</i> Kramer 1911	P	D (Séguy 1941b)
<i>pulla</i> Aldrich 1916	Ne	S
<i>pumila</i> Meigen 1826	P	S
<i>pusana</i> Senior-White 1924	O	T (S.-White et al. 1940)
<i>rostrata</i> Pandellé 1896	P	D (Séguy 1941b)
<i>ruficornis</i> (Fabricius) 1794	No,O,E	D (Lopes 1945c)
<i>santos-diasi</i> Zumpt 1951	E	T (Zumpt 1951)
<i>sarraceniae</i> Riley 1873	Ne	S
<i>sarracenioides</i> Aldrich 1916	Ne	S
<i>schineri</i> Bezzi 1891	P	D (Séguy 1941b)
<i>schnabli</i> Villeneuve 1911b	P	T (Séguy 1941b)
<i>schutzei</i> Kramer 1909	P	T (Séguy 1941b)
<i>scoparia</i> Pandellé 1896	P,O	D (Séguy 1941b)
<i>scoparia nearctica</i> Parker 1916c	Ne	S
<i>scopariformis</i> Senior-White 1927	O	D (S.-White et al. 1940)
<i>semimarginalis</i> Hall 1931	Ne	T (Hall 1931)
<i>sera</i> Rohdendorf 1930	O	D (S.-White et al. 1940)
<i>serbica</i> Baranoff 1930	P	T (Séguy 1941b)
<i>setinervis</i> Rondani 1861b	P	T (Séguy 1941b)
<i>setipennis</i> Rondani 1861b	P	T (Séguy 1941b)
<i>setosa</i> Baranoff 1929	P	D (Séguy 1941b)

<i>sima</i> Aldrich 1916	Ne	S
<i>similis</i> Meade 1876	P,O	D (Séguy 1941b)
<i>sinuata</i> Meigen 1828	Ne,P	S
<i>soror</i> Rondani 1861b	P	S
<i>spinosa</i> Villeneuve 1912b	P	D (Séguy 1941b)
<i>stackelbergi</i> (Rohdendorf) 1937	P	T (Rohdendorf 1937)
<i>strenua</i> Robineau-Desvoidy 1863	P	T (Séguy 1941b)
<i>subdiscalis</i> Aldrich 1916	Ne	D (Aldrich 1916)
<i>subdistinguendis</i> Zumpt 1950b	E	T (Zumpt 1950b)
<i>subulata</i> Pandellé 1896	P	T (Séguy 1941b)
<i>subvicina</i> Rohdendorf 1937	P	T (Séguy 1941b)
<i>surcoufi</i> Villeneuve 1912a	P	T (Séguy 1941b)
<i>synia</i> Johnston & Hardy 1923	A	D (Johnston & Hardy 1923)
<i>talonata</i> Senior-White 1925	O	D (S.-White et al. 1940)
<i>tarsata</i> Aldrich 1916	Ne	S
<i>teretirostris</i> Pandellé 1896	P	D (Séguy 1941b)
<i>tetra</i> Aldrich 1916	Ne	S
<i>thammeri</i> Böttcher 1913a	P	T (Séguy 1941b)
<i>thatuna</i> Aldrich 1916	Ne	S
<i>tibialis</i> Macquart 1850	P,E	D (Séguy 1941b)
<i>transcalensis</i> Zumpt 1950a	E	D (Zumpt 1950a)
<i>tryoni</i> Johnston & Tiegs 1921	A	T (Johnston & Hardy 1923)
<i>tsushimae</i> Senior-White 1924	P	D (S.-White et al. 1940)
<i>uamensis</i> Zumpt 1951	E	T (Zumpt 1951)
<i>uliginosa</i> Kramer 1908a	Ne,P	D (Séguy 1941b)
<i>vagans</i> Meigen 1826	P	S
<i>vansoni</i> Zumpt 1950b	E	T (Zumpt 1950b)
<i>vicina</i> Macquart 1835	P	T (Séguy 1941b)
<i>villa</i> Curran 1934a	E	D (Curran 1934a)
<i>villeneuveana</i> Enderlein 1928a	P	T (Séguy 1941b)
<i>villeneuvei</i> Böttcher 1912c	P	D (Séguy 1941b)
<i>walayari</i> Senior-White 1924	O	D (S.-White et al. 1940)
<i>zeta</i> Johnston & Tiegs 1921	A	D (Johnston & Hardy 1923)
<i>zuluensis</i> Zumpt 1950b	E	D (Zumpt 1950b)

SUBTRIBE RAVINIINA

This group of three genera is almost exclusively New World in distribution. It represents a line of development in which the primitive ventral sclerotization has given rise to a free median process and lateral arms. This triad and its modifications have moved upward into the corpus and do not project. The phallopore and phallus are fused and the corpus is partly or completely closed over ventrally. See Chart 6 for the evolution of the genera and species and Chart 3 for its relationship to the other subtribes and Chart 6 for the evolution of its genera and species.

Genus *Ravinia* Robineau-Desvoidy

Ravinia Robineau-Desvoidy 1863. Hist. Dipt. II 434. Genotype *Sarcophaga haematodes* Meig. equals *Musca striata* Fabr.

- Punasarcophaga** Townsend 1915c. Proc. U. S. Nat. Mus. 49:408. Genotype *Punasarcophaga auromaculata* Tns.
- Andinoravinia** Townsend 1917b. Proc. Biol. Soc. Wash. 30:120. Genotype *Andinoravinia rufipes* Tns.
- Chaetoravinia** Townsend 1917b. Proc. Biol. Soc. Wash. 30:190. Genotype *Helicobia quadrisetosa* Coq. equals *Sarcophaga stimulans* Walk.
- Euravinia** Townsend 1917b. Proc. Biol. Soc. Wash. 30:191. Genotype *Myophora Therminieri* H. D.
- Miltoravinia** Townsend 1917b. Proc. Biol. Soc. Wash. 30:191. Genotype *Sarcophaga planifrons*. Ald.
- Trixosarcophaga** Townsend 1917b. Proc. Biol. Soc. Wash. 30:191. Genotype *Sarcophaga aurigena* Tns. (♀)
- Catasarcophaga** Townsend 1927. Rev. Mus. Paulista 15:220. Genotype *Catasarcophaga trivittata* Tns. (♀) teste Lopes 1941.
- Engelina** Enderlein 1928a. Klass. Sarc.:16. Genotype *Sarcophaga xanthopyga* End. nec. Wulp equals *Andinoravinia rufipes* Tns. teste Townsend 1938.

Frontal bristles generally parallel or but slightly divergent; divergent in last 2 bristles in some species; outer verticals variable; 2 post-ocular rows; 3 or 4 PSDC; anterior acrosticals well developed; 6 to 11 hypopleurals; scutellars 2 or 3-1-0; 2A with only laterals; 3A with MM; 5S deeply incised; brush of short bristles along inner margin of sternal arms, Figs. 234, 235; no sternal window; 1V setulose or bare; hind tibiae bare; phallopore and phallus fused, Figs. 220, 233; hillaе, Figs. 217, 233, present; juxta present only in *Ravinia effrenata* (Walk.), Fig. 229; median process short; lateral arms not retained; dorsal rods Figs. 216, 222, present; vesica simple; no lateral filaments.

The distribution of this genus is Nearctic and Neotropical. Of the twenty species discussed by Hall (1927), twelve are Nearctic, five are Neotropical and three are from Central America and the West Indies. *Ravinia striata* (Fabr.) is Palearctic and Oriental.

Most of the members of this genus, whose biology is known, are coprophagous. This includes *R. pusiola*, *R. Therminieri*, *R. sueta*, *R. stimulans*, *R. latisetosa*, *R. laakei*, *R. avida*. Séguéy (1932a) records *R. striata* as a grasshopper parasite and Thompson (1943) lists it from *Oryctes nasicornis*. Van Emden (1950) records *R. errabunda* from *Epilachna* and a questionable record of *R. Therminieri* from *Lachnosterna*. Knipling (1936) has reared some of the species of this genus on meat in the laboratory. James (1947) records a doubtful record of *R. striata* causing gastro-intestinal myiasis. It has also been recorded in cases of wound myiasis.

Included Species

<i>addentata</i> (Hall) 1929a	Ne	D (Hall 1928)
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<i>almeidai</i> (Lopes) 1946c	No	D (Lopes 1946c)
<i>assidua</i> (Walker) 1852	Ne	D (Aldrich 1930)
<i>aureopyga</i> (Hall) 1928	Ne	D (Hall 1928)
<i>auromaculata</i> (Townsend) 1915c	No	D (Hall 1928)
<i>aurigena</i> (Townsend) 1912a	No	S
<i>belforti</i> Prado & Fonseca 1932	No	D (Prado & Fonseca 1932)
<i>coachelensis</i> (Hall) 1931a	Ne	D (Hall 1931a)
<i>dampfi</i> (Lopes) 1946a	Ne	D (Lopes 1946a)
<i>duplicata</i> (Hall) 1928	Ne	D (Hall 1928)
<i>effrenata</i> (Walker) 1860	Ne, No	S
<i>errabunda</i> (Van der Wulp) 1896	Ne	S
<i>floridensis</i> (Aldrich) 1916	Ne	S
<i>globulus</i> (Aldrich) 1916	No	D (Hall 1928)
<i>laakei</i> (Hall) 1931a	Ne	S
<i>latisetosa</i> Parker 1914b	Ne	S
<i>therminieri</i> (Robineau-Desvoidy) 1830	Ne	S
<i>meinckei</i> (Blanchard) 1939	No	D (Blanchard 1939)
<i>obscuripes</i> (Hall) 1928	Ne	D (Hall 1928)
<i>ollantaytambensis</i> (Hall) 1928	No	D (Hall 1928)
<i>pectinata</i> (Aldrich) 1916	Ne	S
<i>planifrons</i> (Aldrich) 1916	Ne	S
<i>pusiola</i> (Van der Wulp) 1896	Ne	S
<i>querula</i> (Walker) 1837	Ne	S
<i>rufipes</i> (Townsend) 1917b	No	D (Hall 1928)
<i>stimulans</i> (Walker) 1849	Ne	S
<i>striata</i> (Fabricius) 1794	P, O	D (Séguy 1941b)
<i>sueta</i> (Van der Wulp) 1896	Ne	S
<i>tancituro</i> Roback 1952	No	S
<i>trivittata</i> (Townsend) 1927	No	D
<i>vagabunda</i> (Van der Wulp) 1895	Ne	D (Lopes 1946a)

Genus *Oxysarcodexia* Townsend

Oxysarcodexia Townsend 1917b. Proc. Biol. Soc. Wash. 30:191, 194, 195. Genotype *Sarcophaga peltata* Ald.

Dasyproctia Enderlein 1928a. Klass. Sarc.:23. Genotype *Sarcophaga praevolans* End. nec. Wulp equals *Sarcophaga ochripyga* Wulp teste Tns.

Frontal bristles only slightly divergent; outer verticals absent; three post-ocular rows; 3-5 PSDC; if 4 or 5 not all equally developed; 6 to 12 hypopleurals; scutellars 2 or 3-1-0; a weak pair of apicals sometimes present; 2A with only laterals; 3A with MM, lacking in *O. peltata* (Ald.); 5S deeply incised; brush on sternal arms poorly developed, Figs. 263, 265; no sternal windows; IV bare; hind tibiae generally bare; phallophore and phallus fused, Fig. 280; lobi and juxta not present; vesica greatly developed, Figs. 262, 264; lateral arms and thin lateral filaments developed, Figs. 260, 270; dorsal rods present. Genitalia, Figs. 256-280.

Like *Ravinia*, the distribution of *Oxysarcodexia* is essentially New

World. Of the 49 species considered by Lopes (1946) 22 are exclusively South American, and four are North American. The remainder are distributed through various combinations of South America, North America, Central America, and the West Indies. Only *O. taitensis* Schiner has been recorded from some Pacific Islands (Galapagos, Tahiti, Samoa, etc.). It is the dominant genus in southern Brazil.

Not much is known regarding the food habits of the members of this genus. Aldrich (1916) and Wilson (1932) have recorded *O. ventricosa* (Wulp) from cow and horse manure and straw. Luginbill (1928) has recorded it as a parasite of *Laphygma frugiperda*. Both it and *O. galeata* Ald. have been reared from excrement.

Included Species

<i>admixa</i> Lopes 1933	No	D (Lopes 1933)
<i>afficta</i> (Van der Wulp) 1896	Ne,No	D (Lopes 1946b)
<i>amarali</i> Prado & Fonseca 1932	No	D (Prado & Fonseca 1932)
<i>amorosa</i> (Schiner) 1868	No	D (Lopes 1946d)
<i>angolensis</i> Hall 1937a	No	D (Hall 1937a)
<i>angrensis</i> Lopes 1933	No	D (Lopes 1946d)
<i>augusta</i> Lopes 1946d	No	D (Lopes 1946d)
<i>auriceps</i> (Macquart) 1854	No	D (Lopes 1946d)
<i>aurifinis</i> (Walker) 1852	No	D (Lopes 1946d)
<i>avuncula</i> Lopes 1933	No	D (Lopes 1946d)
<i>bakeri</i> (Aldrich) 1916	Ne,No	S
<i>bicolor</i> Lopes 1946d	No	D (Lopes 1946d)
<i>carvalhoi</i> Lopes 1946d	No	D (Lopes 1946d)
<i>cingarus</i> (Aldrich) 1916	Ne	S
<i>comparilis</i> (Reinhard) 1939	Ne	D (Reinhard 1939)
<i>confusa</i> Lopes 1946a	No	D (Lopes 1946d)
<i>culminata</i> (Aldrich) 1926	Ne,No	D (Lopes 1946d)
<i>cyaniforceps</i> (Hall) 1933a	No	D (Lopes 1946d)
<i>diana</i> Lopes 1933	No	D (Lopes 1946d)
<i>edwardsi</i> Lopes 1946d	No	D (Lopes 1946d)
<i>flavifrons</i> (Macquart) 1846	No	D (Lopes 1946d)
<i>fluminensis</i> Lopes 1946d	No	D (Lopes 1946d)
<i>fringidea</i> (Curran & Walley) 1934	No	D (Lopes 1946d)
<i>galeata</i> (Aldrich) 1916	Ne	S
<i>grandis</i> Lopes 1946d	No	D (Lopes 1946d)
<i>illata</i> Lopes 1938b	No	D (Lopes 1938b)
<i>insolita</i> Lopes 1946d	No	D (Lopes 1946d)
<i>intona</i> (Curran & Walley) 1934	No	D (Lopes 1946d)
<i>major</i> Lopes 1946d	No	D (Lopes 1946d)
<i>megista</i> (Hall) 1933a	No	D (Lopes 1946d)
<i>meridionalis</i> (Engel) 1931	No	D (Lopes 1946d)
<i>modesta</i> Lopes 1946d	No	D (Lopes 1946d)
<i>molitor</i> (Curran & Walley) 1934	No	D (Lopes 1946d)
<i>occulta</i> Lopes 1946d	No	D (Lopes 1946d)
<i>ochripyga</i> (Van der Wulp) 1896	Ne,No	S
<i>omissa</i> Lopes 1946a	Ne	D (Lopes 1946a)

<i>parva</i> Lopes 1946d	No	D (Lopes 1946d)
<i>peltata</i> (Aldrich) 1916	Ne, No	S
<i>perneta</i> (Walker) 1860	Ne	D (Lopes 1946d)
<i>plaumanni</i> Lopes 1946d	No	D (Lopes 1946d)
<i>plebeja</i> Lopes 1946a	No	D (Lopes 1946d)
<i>ramosa</i> (Reinhard) 1939	No	D (Reinhard 1939)
<i>riograndensis</i> Lopes 1946d	No	D (Lopes 1946d)
<i>sanguisuga</i> (Hall) 1933a	No	D (Lopes 1946d)
<i>simplicoides</i> Lopes 1933	No	D (Lopes 1946d)
<i>taitensis</i> (Schiner) 1868	A, Oc	D (Lopes 1946d)
<i>timida</i> Aldrich 1916	Ne, No	D (Aldrich 1916)
<i>titubata</i> Lopes 1946c	No	D (Lopes 1946c)
<i>titubata fraterna</i> Lopes 1946a	Ne	D (Lopes 1946a)
<i>trivialis</i> (Van der Wulp) 1896	Ne	S
<i>ventricosa</i> (Van der Wulp) 1896	Ne, No	S
<i>vesica</i> (Hall) 1933a	No	D (Lopes 1946d)
<i>xanthosoma</i> (Aldrich) 1916	Ne, No	S

Genus *Cistudinomyia* Townsend

Cistudinomyia Townsend 1917a. Proc. Biol. Soc. Wash. 30:48. Genotype *Sarcophaga cistudinis* Ald.

Frontal bristles barely divergent; outer verticals hardly distinct; 3 post-ocular rows; 4-5 PSDC; anterior acrosticals hardly differentiated; scutellars 3 or 4-1-0; 2A with only laterals; 3A with marginal rows of 20; 1V bare; hind tibiae bare; 5S broad with shallow V, Fig. 287; phallopore and phallus fused; vesica claw-shaped in profile, Fig. 286; median process and lateral arms present, Fig. 285; no juxta, filaments, or dorsal rods.

The only species, the genotype above, is recorded only from the United States. Aldrich (1916) records it from New Jersey and the author has seen specimens from Texas.

Aldrich (1916) records *C. cistudinis* as being bred from sores in the side of a box turtle. Knipling (1937) has worked out the biology and immature stages.

SUBTRIBE HYSTRICOCNEMINA

Like *Imparia* Roback and *Hypopelta* Ald. the genus *Hystricocnema* is unique. The corpus is long and expanded laterally toward its apex, Figs. 281, 283; it possesses a median process and lateral filaments. The lateral filaments, Fig. 284, resemble those of *Sarcophaga fulvipes* Macq., Fig. 192. The nature of the fifth sternite and the phallus indicate a separate origin from the early sarcophagine-raviniine stock and this genus is given subtribal rank here. See Chart 3.

Genus *Hystricocnema* Townsend

Hystricocnema Townsend 1919. Ins. Ins. Mens. VI:160. Genotype *Sarcophaga robusta* Ald. equals *Sarcophaga plinthopyga* Wied.

Frontal row slightly divergent in last 2 bristles; outer verticals absent;

2 post-ocular rows; generally 5 PSDC; anterior 2 small, the remaining 3 larger; anterior acrosticals barely differentiated; scutellars 2-1-1; 2A and 3A with only laterals; IV and hind tibiae bare; a few long hairs sometimes present; 5S as in Fig. 282; anal forceps vertically bipronged, basal part extended vertically; phallus as in Figs. 281, 283.

The genotype is the only species in the genus. *Sarcophaga khalili* Salem 1935 is a synonym of *S. robusta* (Ald.) according to Salem (1936). *H. plinthopyga* is found in southern and western United States, Central and South America, Galapagos, and Hawaii. It has been reared from carrion, Aldrich (1916). Thompson (1943) lists it from *Lachnosterna*. James (1947) cites cases of it as a myiasis producer in man and animals.

Series 3

In this series, the ventral sclerotization undergoes modification without division (Sarcodexiina and Servaisiina) or divides after it has undergone modification (Boettcheriina). Of those species in this series whose biology is known, most are true parasites. There are no species with two notopleurals or proclinate fronto-orbitals in the male.

This series contains three subtribes. These are Sarcodexiina, Boettcheriina, and Servaisiina. See Chart 3 for the relationships of these subtribes.

SUBTRIBE SARCODEXIINA

This subtribe consists of three genera which are held together by possessing median filaments. The vesica is present or absent and a juxta is present only in *Sarcodexia* Tns. All the members of this subtribe are New World in distribution, being found in South America, Central America and the West Indies, and southern United States. Very little is known concerning the biology of most of the species.

See Chart 3 for the relationship of this subtribe to the others, and Chart 7 for the evolution of its genera and species.

Genus *Paraphrissopoda* Townsend

Paraphrissopoda Townsend 1915b. Ins. Ins. Mens. 3:118. Genotype *Peckia lamanensis* R.-D. equals *Musca gulo* Fab.

Chrysostomyia Townsend 1931b. Rev. Ent. Rio de Janeiro. 1:315. Genotype *Sarcophaga chrysostoma* Wied.

Frontal row divergent in last 2 or 3 bristles; outer verticals absent; 3 post-ocular rows; PSDC 5 or 6; 3 or 4 small and 2 large; anterior acrosticals lacking; 8 to 11 hypopleurals; scutellars 2 or 3-0-1; 2A with only laterals; 3A with or without MM; IV bare; hind tibiae villous; 5S as in Figs. 288, 295, 296; median filaments present; harpes present in some, Figs. 290, 294; vesica present; juxta absent; anal forceps often long and

slightly sinuate in profile; genitalia, Figs. 288-301; see Chart 7 for relationships and evolution.

All the known species in this genus occur in the New World, being found in the southern United States, Panama, West Indies, and South America.

Very little is known of their biology. Lopes (1943) has reared *P. chrysostoma* on meat in the laboratory. James (1947) cites it as a myiasis producer.

Included Species

<i>amoena</i> (Aldrich) 1916	No	S
<i>bergi</i> (Blanchard) 1939	No	D (Blanchard 1939)
<i>capitata</i> (Aldrich) 1916	No	S
<i>chrysostoma</i> (Wiedemann) 1830	No	S
<i>chrysostomata</i> (Hall) 1933a	No	T (Hall 1933a)
<i>concinata</i> (Williston) 1896	No	D (Aldrich 1916)
<i>enderleini</i> (Engel) 1931	No	T (Engel 1931)
<i>gulo</i> (Fabricius) 1805	No	S
<i>hillifera</i> (Aldrich) 1916	No	S
<i>hirsuta</i> (Hall) 1933a	No	T (Hall 1933a)
<i>lithogaster</i> (Curran and Walley) 1934	No	T (Curran and Walley 1934)
<i>nephele</i> Lopes 1941	No	T (Lopes 1941)
<i>pexata</i> (Van der Wulp) 1896	Ne, No	T (Aldrich 1930)
<i>setifacies</i> Lopes 1945a	No	T (Lopes 1945a)
<i>spectabilis</i> (Aldrich) 1916	Ne	D (Aldrich 1916)
<i>unicinata</i> (Hall) 1933a	No	T (Hall 1933a)

Genus *Euboettcheria* Townsend

Euboettcheria Townsend 1927. Rev. Mus. Paulista. 15:231. Genotype *Euboettcheria australis* Tns.

Ctenolioproctia Enderlein 1928a. Klass. Sarc., p. 27. Genotype *Ctenolioproctia venusta* End. equals *Euboettcheria australis* Tns.

Frontal row divergent in last 3 bristles; outer verticals absent; 3 post-ocular rows; PSDC 4 weak—2 strong; 8 hypopleurals; scutellars 3-0-1; 2A with laterals only; 3A with MM; 1V bare; hind tibiae villous; 5S as in Fig. 306; corpus tubular, greatly elongated, Fig. 307; median filaments present; no juxta or vesica.

All the members of this genus, as far as is known, are Mexican and South American and from the West Indies. The biology is not known.

Included Species

<i>anguilla</i> (Curran and Walley) 1934	No	T (Curran and Walley 1934)
<i>asinoma</i> Hall 1938	No	D (Hall 1938)
<i>australis</i> Townsend 1927	No	S
<i>collusor</i> (Curran and Walley) 1934	No	T (Curran and Walley 1934)
<i>epimelia</i> (Lopes) 1938a	No	D (Lopes 1938a)

<i>florencioi</i> (Prado and Fonseca) 1932	No	T (Prado and Fonseca 1932)
<i>naides</i> Lopes 1941	No	D (Lopes 1941)
<i>nicasia</i> Lopes 1941	No	D (Lopes 1941)
<i>percussa</i> (Lopes) 1938b	No	T (Lopes 1938b)
<i>volucris</i> (Van der Wulp) 1896	Ne	T (Aldrich 1930)

Genus *Sarcodexia* Townsend

Sarcodexia Townsend 1892c. Jour. Inst. Jam. 1:105. Genotype *Sarcodexia sternodontis* Tns. equals *Sarcophaga lambens* Wied.

Cricobrachia Enderlein 1928a. Klass. Sarc., p. 19. Genotype *Cricobrachia anisitsiana* End. congeneric with *S. sternodontis* Tns. teste Tns. 1938. Aldrich (1930) mentions that Townsend saw Enderlein's type and considered them as synonyms.

Frontal row divergent in last 2 bristles; outer verticals absent; 3 post-ocular rows; 4 PSDC; anterior acrosticals present; scutellars 2-1-1; 2A with only laterals; 3A with MM to row; IV bare; hind tibiae bare; 5S as in Fig. 303; median filaments present; juxta large and complex; forked from its base, Fig. 302; no vesica.

This is a West Indian and South American species. It also occurs in southern United States. It has been reared from Coleoptera, Orthoptera, and Lepidoptera, Aldrich (1916). Thompson (1943-47) lists it as parasitic on *Strategus* and various Hemiptera and Lepidoptera. McCallan (1947) also lists it from Lepidoptera (*Sacadodes pyralis*). James (1947) cites cases of it as a myiasis producer and also mentions its being reared from carrion and dung.

SUBTRIBE BOETTCHERIINA

This subtribe is characterized by possessing median process and lateral filaments which are formed from the ventral sclerotization and are well developed before they split apart (see Chart 3). This distinguishes it from the Sarcophagina and Raviniina where the split takes place first. Also here the median process is always free, never fused to the juxta as in the Sarcophagina. The juxta is present in all but a few aberrant genera. The anterior juxtal process is present only in a few genera of this subtribe.

As far as is known, the Boettcheriina is entirely New World in distribution.

Little is known concerning the biology of the species. Those that are known are mainly parasitic.

See Chart 8 for the evolution of the genera and species.

Genus *Rafaelia* Townsend

Rafaelia Townsend 1917a. Proc. Biol. Soc. Wash., 30:45. Genotype *Rafaelia rufiventris* Tns.

Frontal bristles barely divergent; outer verticals present; 2 post-ocular

rows; 3 PSDC; anterior acrosticals present or absent; 4 to 7 hypopleurals; scutellars 3-1-0 or 2-1-1; 2A with laterals only; 3A with MM; 1V setulose; hind tibiae bare; juxta small; median process and lateral filaments connected, Figs. 311, 314; vesica poorly developed, plate-like, Figs. 310, 313.

This genus is North American in distribution. The biology is not known.

Included Species

<i>ampulla</i> (Aldrich) 1916	Ne	S
<i>rufiventris</i> Townsend 1917a	Ne	S

Genus **Metoposarcophaga** Townsend

Frontal row hardly divergent to divergent in last 3 bristles; outer verticals present; 3 or 4 post-ocular rows; 3 or 4 PSDC; anterior acrosticals present; 6 to 9 hypopleurals; scutellars generally 2 or 3-1-0; weak apicals sometimes present; 2A with only laterals; 3A with or without MM; 1V setulose or bare; hind tibiae villous or bare; 5S with short base and no window, Fig. 320, 325; phallopore hooked behind at base, Figs. 316, 326; corpus capsule-like and smoothly surfaced; often projecting caudally; Figs. 316, 327; juxta and free median process and lateral filaments present; vesica connate and plume-like, Figs. 316, 324; genital segments greatly protuberant, Fig. 460; anal plates large, Figs. 333, 334.

Key to Subgenera—Males

1. 3 posterior dorsocentrals; hind tibiae bare. **Metoposarcophaga**
- 4 posterior dorsocentrals; hind tibiae villous. **Zygastropyga**

Subgenus **Metoposarcophaga** Townsend

Metoposarcophaga Townsend 1917a. Proc. Biol. Soc. Wash. 30:46.

Genotype *Sarcophaga pachyprocta* Park. equals *Sarcophaga importuna* Walk.

Frontal row barely divergent; 3 PSDC; hind tibiae bare, 1V setulose; corpus rounded, not much produced behind; Fig. 324; juxta narrow and bifurcate, Fig. 324; vesica with brush of upcurved bristles and hairs; 5S as in Fig. 321.

Both species in this subgenus are North American as far as is known at present. *M. importuna* has been bred from terrapin eggs, Aldrich (1916).

Included Species

<i>importuna</i> (Walker) 1848	Ne	S
<i>pachyproctosa</i> Parker 1919a	Ne	D (Parker 1919a)

Subgenus **Zygastropyga** Townsend

Zygastropyga Townsend 1917b. Proc. Biol. Soc. Wash. 30:191. Genotype *Zygastropyga aurea* Tns.

Thelylepticocnema Townsend 1917a. Proc. Biol. Soc. Wash. 30:43. Genotype *Sarcophaga incurva* Ald.

Sabinata Parker 1921. Proc. Brook. Ent. Soc. 16:112. Genotype *Sabinata catalina* Park. equals *Sarcophaga villipes* Wulp.

Frontals barely divergent or divergent in last 2 or 3 bristles; 4 PSDC; scutellars 2 or 3-1-0; IV bare or setulose; hind tibiae villous; juxta broad and fused, Fig. 326; or small and free, Fig. 317; corpus generally projecting behind; 5S as in Figs. 320, 325, 328; vesica with plumosity coarse, branch-like, Figs. 316, 326.

All the species placed here are North American in distribution. Their biology is not known.

Included Species

<i>aldrichi</i> (Parker) 1921	Ne	D (Parker 1921)
<i>arizonica</i> (Parker) 1921	Ne	D (Parker 1921)
<i>aurea</i> Townsend 1917b	Ne	S
<i>cantenea</i> (Roback) 1952	Ne	S
<i>incurva</i> (Aldrich) 1916	Ne	D (Aldrich 1916)
<i>sulculata</i> (Aldrich) 1916	Ne	S
<i>tothilli</i> Parker 1919a	Ne	D (Parker 1919a)
<i>villipes</i> (Van der Wulp) 1896	Ne	S

From Aldrich's (1930) description of *Tripanurga* B & B, type *Sarcophaga albicans* (Wied.), it appears that this genus will probably fall within the genus *Metoposarcophaga*. It differs from *Metoposarcophaga* in the possession of proclinate fronto-orbitals in the male and the lack of anterior acrosticals. The figures of the genitalia, however, seem to place it very close to the subgenus *Zygastropyga*. Should a future examination of specimens of *Sarcophaga albicans* place it within *Metoposarcophaga*, then *Metoposarcophaga* Tns. will fall to *Tripanurga* B & B.

Genus *Aphelomyia* new genus

Frontal row divergent in last 3 bristles; outer verticals not well developed, 3 post-ocular rows; 4 PSDC; anterior acrosticals present; scutellars 3-1-0; pair of weak apicals may be present; 2A with only laterals; 3A with only laterals; IV bare; hind tibiae bare; 5S with short base and narrow arms, Fig. 332; corpus small, barrel-shaped, Fig. 330, vesica plumose, similar to *Metoposarcophaga*; genitalia as in Figs. 330-332.

Genotype and only species, *Sarcophaga welchi* Hall by present designation.

This species was described from Cuba and Florida. Its biology is unknown. Though aberrant for the subtribe Boettcheriina, it is placed here on the basis of the resemblance of its vesica to that of *Metoposarcophaga* Tns.

Genus *Boettcheria* Parker

Boettcheria Parker 1914b. Proc. Bost. Soc. Nat. Hist. 35:65. Genotype *Boettcheria latisterna* Park.

Parasarcodexia Townsend 1917b. Proc. Biol. Soc. Wash. 30:192. Genotype *Sarcophaga parkeri* Ald.

Frontal row sharply divergent in last 4 or 5 bristles; outer verticals variable; 4 post-ocular rows; 3 PSDC; anterior acrosticals present; scutellars 2 or 3-1-1; 2A with laterals only; 3A generally with MM or row; IV bare; hind tibiae bare or villous; 5S, Figs. 338, 344, deeply incised; vesica well developed, often very large and bizarre, Figs. 341, 346; median process and lateral filaments present; lateral filaments often very long and narrow, Fig. 346; phallopore and phallus partially fused.

Lopes (1950b) has summarized all the known data on the species of this genus. Only *B. carata* Roback can be added to his list of species.

Genus *Spirobolomyia* Townsend

Spirobolomyia Townsend 1917a. Proc. Biol. Soc. Wash. 30:43. Genotype *Sarcophaga singularis* Ald. equals *Sarcophaga pallipes* Walk. teste Tns. (1938).

Frontal row divergent in last 2 or 3 bristles; outer verticals absent; 3 post-ocular rows; 4 or 5 PSDC; anterior acrosticals present; scutellars 2-1-1; 2A with laterals only; 3A with MM; IV bare; hind tibiae villous or bare; 5S as in Figs. 351, 354, 361, corpus hooked below, shaped as reversed K, Figs. 350, 352, 360; semi-sclerous foliate lateral plates present; median process and lateral filaments long and tubular; juxta small, Figs. 355, 360.

All three species are North American. *S. pallipes* (Walk.) has been reared from *Sparobolus* sp., Aldrich (1916) and *Julus* sp., Townsend (1917a, p. 43). *S. flavipalpis* (Ald.) has been also reared from *Sparobolus* sp., Aldrich (1916).

Included Species

<i>basalis</i> (Walker) 1852	Ne	S
<i>flavipalpis</i> (Aldrich) 1916	Ne	S
<i>pallipes</i> (Walker) 1852	Ne	S

Genus *Kellymyia* Townsend

Kellymyia Townsend 1917b. Proc. Biol. Soc. Wash. 30:191. Genotype *Sarcophaga kellyi* Ald.

Frontal row divergent in last 3 bristles; outer verticals absent; 4 post-ocular rows; 4 PSDC; anterior acrosticals present; scutellars 2-1-1; 2A with only laterals; 3A with complete row; IV and hind tibiae bare; 5S as in Fig. 308; corpus thin and apically curved in profile, Fig. 309; lateral plates vertically ovate, semi-sclerous, foliate, Fig. 309; no median process or filaments.

Though aberrant for the subtribe, *Kellymyia* is placed close to *Spirobolomyia* on the basis of the lateral plates.

The genotype is the only species and is a common North American

grasshopper parasite. Thompson (1943) lists it as a parasite of *Glossina palpalis* in the Upper Congo (?). Van Enden (1950) records it from *Asida*, *Eleodes*, and *Plectodera*.

Genus *Cucullomyia* new genus

Frontal row barely divergent; outer verticals present; 2 post-ocular rows; 3 PSDC; anterior acrosticals absent; scutellars 2-1-0; 2A with only laterals; 3A with MM; 1V and hind tibiae bare; 5S as in Fig. 365; corpus with a roof-like semi-sclerous projection; juxta small; median process and lateral filaments small; phallus as in Fig. 362-364.

Genotype and only species *Sarcophaga pedunculata* Hall by present designation. The genitalia are different from any other known Sarcophagini. It is North American and the biology is unknown.

Genus *Tylomyia* new genus

Frontal row barely divergent; outer verticals present; 2 post-ocular rows; 4 PSDC; anterior acrosticals absent; scutellars 3-1-0; 2A with only laterals; 3A with MM; 1V setulose; hind tibiae bare; 5S as in Fig. 356; phallus large and striking, Fig. 357; median process and lateral filaments thick, elongate and knobbed distally, Figs. 357, 359.

Genotype and only species *Sarcophaga texana* Ald. by present designation.

It is a North American species and has been bred from animal carcasses and meat, Aldrich (1916).

SUBTRIBE SERVAISIINA

This subtribe is characterized by the modification of the ventral sclerotization without any division. The limen (*Acandotheca*), the cunabula (*Servaisia*), and the stemmatis (*Fletcherimyia*) are the structures developed in each of the three genera of this subtribe. Most of its members are parasites. See Chart 9 for the evolution of the genera and species of this subtribe.

Genus *Fletcherimyia* Townsend

Fletcherimyia Townsend 1917b. Proc. Biol. Soc. Wash. 30:191. Genotype *Sarcophaga fletcheri* Ald.

Peltopyga Townsend 1917b. Proc. Biol. Soc. Wash. 30:191. Genotype *Sarcophaga celarata* Ald.

Frontal row divergent in last 2 or 3 bristles; outer verticals present or absent; 3 or 4 post-ocular rows; 3 or 4 PSDC; a small fifth may be present; anterior acrosticals absent; 7 hypopleurals; scutellars 2-1-1; discal and apical may be absent in *F. fletcheri*; 2A with MM in *F. fletcheri*; 3A with MM in all species; hind tibiae bare; 1V bare; 5S deeply incised with secondary internal peak, Figs. 369, 371, 373; stemmatis present, Figs.

370, 376; juxta two broad, lightly colored flaps, haired dorsally, Figs. 366, 367.

All the species are found in eastern North America and live in the cups of species of *Sarracenia*. They apparently feed on both dead and living insects in the cups.

Included Species

<i>celarata</i> (Aldrich) 1916	Ne	S
<i>fletcheri</i> (Aldrich) 1916	Ne	S
<i>jonesi</i> (Aldrich) 1916	Ne	S
<i>rileyi</i> (Aldrich) 1916	Ne	S

Genus *Kurtomyia* new genus

Frontal rows sharply divergent in last 2 or 3 bristles; outer verticals vestigial; ocellars small; 3 post-ocular rows; 3 PSDC; 2 or 3 anterior acrosticals; scutellars 2-1-1; apicals small; propleura bare; 2A and 3A with only lateral bristles; hind tibiae moderately villous; 1V bare; corpus thin in profile, curved forward apically, Fig. 410; slightly divided at apex in frontal view, Fig. 409; vesica divided, Fig. 409.

Genotype *Sarcophaga postilla* Reinhard by present designation.

The genitalia show no relationship to any other known Sarcophagini. The fifth sternite is very much like those found in the genera *Servaisia* and *Acandotheca* and places this genus near them within the Servaisiina.

Genus *Servaisia* Robineau-Desvoidy

Frontal row divergent in last 2 or 3 bristles; outer verticals generally absent; 3 or 4 post-ocular rows; 3 or 4 PSDC; anterior acrosticals generally present; scutellars 2 or 3-1-1; 2A with laterals only; 3A with MM to row; hind tibiae bare; 1V bare; anal forceps indented at base, Fig. 456, or reverse L-shaped, Fig. 458; spines or hairs on outer side below; cunabula, Figs. 382, 384, 385, 396, present; explanate vesica, Figs. 382, 392, and juxta, Figs. 396, 398, 403, present or absent; 5S with short base and bumps on inner edges of sternal arms, Figs. 394, 404.

The members of this genus are united in the possession of the cunabula by all and the explanate vesica by most of its members. Each of the subgenera represents a line of development within the genus. See Chart 9.

The following species have been placed in the genera *Sarcophaga* Meig., *Blaesoxipha* Loew, *Locustaevora* Rohd., and *Gesneroides* Vill. At present they cannot be definitely placed in any of the subgenera proposed here. Most will fall in the genus *Servaisia* but a few, as is the case with *B. arenicola* Rohd., will fall in *Acandotheca*. Should *B. laticornis* Meig. (equals *grylloctona* Loew) prove to be congeneric under the generic concepts proposed here, then *Servaisia* R.-D. will fall to *Blaesoxipha* Loew.

Included Species

<i>acuminata</i> (Villeneuve) 1912d	P	T (Séguy 1941b)
<i>alopecis</i> (Reinhard) 1947	Ne	T (Reinhard 1947)
<i>asiatica</i> (Rohdendorf) 1928c	P	T (Séguy 1941b)
<i>aurulenta</i> (Rohdendorf) 1937	P	T (Rohdendorf 1937)
<i>baranoffi</i> (Senior-White) 1940	O	T (S.-White et al. 1940)
<i>battiligera</i> (Séguy) 1941b	P	T (Séguy 1941b)
<i>binodonosa</i> (Curran) 1934a	E	T (Curran 1934a)
<i>carinata</i> (Rohdendorf) 1937	P	T (Rohdendorf 1937)
<i>cinereogrisea</i> (Rohdendorf) 1937	P	T (Rohdendorf 1937)
<i>cochlearis</i> (Pandellé) 1896	P	T (Séguy 1941b)
<i>confusa</i> (Villeneuve) 1912d	P	T (Séguy 1941b)
<i>convexa</i> (Reinhard) 1947	Ne	T (Reinhard 1947)
<i>fasciventris</i> (Curran) 1934a	E	T (Curran 1934a)
<i>filipjevi</i> (Rohdendorf) 1928a	P	T (Séguy 1941b)
<i>flavipes</i> (Aldrich) 1916	Ne	T (Aldrich 1916)
<i>fossoria</i> (Pandellé) 1896	P	T (Séguy 1941b)
<i>fridolini</i> (Rohdendorf) 1937	P	T (Rohdendorf 1937)
<i>gemina</i> (Hardy) 1943	A	T (Hardy 1943)
<i>gladatrix</i> (Pandellé) 1896	P	T (Séguy 1941b)
<i>jakovlevi</i> (Rohdendorf) 1937	P	T (Rohdendorf 1937)
<i>kastneri</i> (Baranoff) 1932	O	T (S.-White et al. 1940)
<i>koslovi</i> (Rohdendorf) 1937	P	T (Rohdendorf 1937)
<i>laticornis</i> (Meigen) 1826	P	T (Séguy 1941b)
<i>lindneri</i> (Rohdendorf) 1937	P	T (Rohdendorf 1937)
<i>lineata</i> (Fallén) 1816	P	T (Séguy 1941b)
<i>litoralis</i> (Villeneuve) 1911b	P	T (Séguy 1941b)
<i>migratoriae</i> (Rohdendorf) 1928c	P	T (Séguy 1941b)
<i>occatrix</i> (Pandellé) 1896	P	T (Séguy 1941b)
<i>pagella</i> (Reinhard) 1947	Ne	T (Reinhard 1947)
<i>popovi</i> (Rohdendorf) 1937	P	T (Rohdendorf 1937)
<i>putilla</i> (Reinhard) 1947	Ne	T (Reinhard 1947)
<i>pygmaea</i> (Zetterstedt) 1845	P	T (Séguy 1941b)
<i>rossica</i> (Villeneuve) 1912d	P	T (Séguy 1941b)
<i>rubripes</i> (Villeneuve) 1912d	P	T (Séguy 1941b)
<i>shelkovnikova</i> (Rohdendorf) 1937	P	T (Rohdendorf 1937)
<i>silantjevi</i> (Rohdendorf) 1937	P	T (Rohdendorf 1937)
<i>subcochlearis</i> (Séguy) 1932b	P	T (Séguy 1941b)
<i>ungulata</i> (Pandellé) 1896	P	T (Séguy 1941b)
<i>unicolor</i> (Villeneuve) 1912d	P	T (Séguy 1941b)
<i>valangae</i> (Aldrich) 1932	O	T (S.-White et al. 1940)
<i>zachvatkini</i> (Rohdendorf) 1937	P	T (Rohdendorf 1937)

The majority of the species in the above list are parasitic on Orthoptera. See Séguy (1932a and 1941b) and Rohdendorf (1932 and 1937) for further details on the biology.

Key to Subgenera—Males

1. Anal forceps short, reverse L-shaped, Fig. 458; large, partly sclerous plates on either side of corpus, Fig. 412 **Speciosia**
 Anal forceps not as above; of normal length and shape; indented

- near base, Fig. 4562
2. Juxta absent; corpus short; cunabula as in Figs. 378, 382 **Protodexia**
Juxta present3
3. Juxta very small; peaked; corpus elongate, constricted before apex,
Fig. 389**Sarpedia**
Juxta well developed; bifurcate and spatulate, Figs. 396, 398; corpus
short4
4. Juxta forked; connected at base, Fig. 396; cunabula as in Figs. 392,
393, 396**Servaisia**
Juxta separated at base, Figs. 403, 406; cunabula large and curved,
Figs. 393, 401**Acridophaga**

Subgenus **Acridophaga** Townsend

Acridophaga Townsend 1917a. Proc. Biol. Soc. Wash. 30:46. Genotype
Sarcophaga aculeata Ald.

Cunabula well formed, curved in profile, Figs. 399, 407; explanate
vesica partly sclerous; juxta completely divided at base.

The members of this subgenus are, as far as is known, all parasitic and
are Nearctic, Neotropical, and Palearctic in distribution. Massini (1919)
has given the biology of *S. caridei*.

Included Species

<i>aculeata</i> (Aldrich) 1916	Ne	S
<i>aculeata gavia</i> (Aldrich) 1916	Ne	D (Aldrich 1916)
<i>aculeata taediosa</i> (Aldrich) 1916	Ne	D (Aldrich 1916)
<i>angustifrons</i> (Aldrich) 1916	Ne	S
<i>caridei</i> (Brèthes) 1906	Ne, No	S
<i>potanini</i> (Rohdendorf) 1928c	P	D (Rohdendorf 1932)
<i>reversa</i> (Aldrich) 1916	Ne	S
<i>websteri</i> (Aldrich) 1916	Ne	D (Aldrich 1916)

Subgenus **Protodexia** Townsend

Protodexia Townsend 1912c. Jour. N. Y. Ent. Soc. 30:117. Genotype
Protodexia synthetica Tns. equals *Sarcophaga hunteri* Hough.

Opsophyto Townsend 1915a. Proc. Biol. Soc. Wash. 28:23. Genotype
Sarcophaga opifera Coq.

Locustivora Johnston and Tiegs 1922a. Proc. Biol. Soc. Queensland.
34:187. Genotype *Masicera pachytyli* Skuse congeneric with *S. opi-*
fera teste Tns. 1938.

Juxta absent; corpus moderately short, Figs. 377, 380; cunabula as in
Figs. 378, 382; explanate vesica present or absent.

The members of this subgenus are all parasitic and Nearctic, and if
Townsend's synonymy is correct, Australian in distribution. Lopes (1943)
has reported *Protodexia* from Brazil.

Included Species

<i>arteagi</i> (Blanchard) 1939	No	T (Blanchard 1939)
<i>hunteri</i> (Coquillett) 1892	Ne	S
<i>hunteri aenigma</i> (Reinhard) 1947	Ne	D (Reinhard 1947)
<i>opifera</i> (Coquillett) 1892	Ne	S
<i>pachytyli</i> (Skuse) 1891	A	D (Hardy 1943)

Subgenus **Sarpedia** new subgenus

Juxta very small, peaked, Fig. 390; corpus elongate, constricted before tip, Fig. 389.

Genotype *Sarcophaga setigera* Ald. by present designation.

S. setigera is Nearctic in distribution and a parasite. Branch (1920) has recorded it from a mantid. It is a web spinner, the only such case known in the Sarcophagini.

Included Species

<i>lorena</i> (Roback) 1952	Ne	S
<i>setigera</i> (Aldrich) 1916	Ne	S

Subgenus **Servaisia** Robineau-Desvoidy

Servaisia Robineau-Desvoidy 1863. Hist. Dipt. 2:429. Genotype *Sarcophaga erythrura* Meigen.

Juxta well developed, Figs. 385, 396, bifurcate, connected at base; explanate vesica and cunabula present; Figs. 383-387 and 391-396.

The members of this subgenus are entirely parasitic. At present its distribution is Nearctic and Palearctic, and when more species can be definitely placed it probably will extend into the Oriental and Australian regions.

Included Species

<i>coloradensis</i> (Aldrich) 1916	Ne	S
<i>erythrura</i> (Meigen) 1826	P	S
<i>falciformis</i> (Aldrich) 1916	Ne	S
<i>formosa</i> (Rohdendorf) 1928a	P	D (Rohdendorf 1928a)
<i>uncata</i> (Van der Wulp) 1896	Ne	S

Subgenus **Speciosia** new subgenus

Well-developed cunabula present, Fig. 412; explanate vesica apparently represented by 2 large lateral plates on either side of corpus; corpus with hook-like projections antero-laterally.

Genotype and only species *Fletcherimyia speciosa* Lopes by present designation.

This is the most aberrant subgenus of *Servaisia*, but the presence of the cunabula and the shape of the fifth sternite, Fig. 411, place it here. It is Nearctic in distribution and the biology is unknown.

Genus **Acandotheca** Townsend

Frontal row divergent in last 2 or 3 bristles; outer verticals variable;

3 or 4 post-ocular rows; 3 or 4 PSDC; anterior acrosticals variable; scutellars 2 or 3-1-1; apicals rarely absent; 2A with only laterals; 3A with MM to complete row; 1V setulose or bare; hind tibiae bare; anal forceps indented near base; spines or hairs on outer side below, Fig. 456; fifth sternite with short base and protuberance on inner edges of sternal arms, Figs. 422, 426, 430; limen present; juxta, explanate vesica and copi, Figs. 427-441, may be present. Figs. 414-431.

The members of this genus are held together by the presence of the limen, the shape of 5S, and the anal forceps. Several lines of development within it are represented by the subgenera. See Chart 9.

Key to Subgenera—Males

1. Copi present, Figs. 427, 448, 432 **Acandotheca**
 Copi absent 2
2. Juxta present **Tephromyiella**
 Juxta absent 3
3. First vein bare; genitalia as in Fig. 414 **Stenolaucotheca**
 First vein setulose 4
4. Three posterior dorsocentrals; explanate vesica present, Figs. 423..
 **Lepyria**
 Four posterior dorsocentrals; vesica present, Fig. 420 **Mecynocorpus**

Subgenus **Acandotheca** Townsend

Acandotheca Townsend 1917c. Ins. Ins. Mens. 5:159. Genotype *Sarcophaga prohibita* Ald.

Eleodiomyia Townsend 1917c. Ins. Ins. Mens. 5:160. Genotype *Sarcophaga eleodis* Ald.

Sarcophodexia Townsend 1917c. Ins. Ins. Mens. 5:161. Genotype *Sarcophaga hamata* Ald.

Notochaetopsis Townsend 1917c. Ins. Ins. Mens. 5:162. Genotype *Sarcophaga masculina* Ald.

Hamatomyia Blanchard 1939. Physis 18:816. Genotype *Hamatomyia denieri* Blanchard.

PSDC 3 or 4; juxta present, tips pointed, Figs. 428, 434; copi present, Figs. 427-441; explanate vesica well developed only in *Acandotheca complosa* (Rein.) and *Acandotheca eleodis* (Ald.)

The species of this subgenus are Nearctic and Neotropical in distribution and, as far as known, mostly parasitic. Van Emden (1950) lists *A. eleodis* from *Asida* and *Eleodes*. Thompson (1943) lists *A. rudis* from *Ligyris* and *A. prohibita* from *Lachnosterna*.

Included Species

<i>alcedo</i> (Aldrich) 1916	Ne	S
<i>complosa</i> (Reinhard) 1947	Ne	S

<i>denieri</i> (Blanchard) 1939	No	D (Blanchard 1939)
<i>eleodis</i> (Aldrich) 1916	Ne	S
<i>excisa</i> (Aldrich) 1916	Ne	D (Aldrich 1916)
<i>hamata</i> (Aldrich) 1916	Ne	S
<i>magna</i> (Aldrich) 1916	Ne	D (Aldrich 1916)
<i>masculina</i> (Aldrich) 1916	Ne	S
<i>prohibita</i> (Aldrich) 1916	Ne	S
<i>reperta</i> (Reinhard) 1947	Ne	D (Reinhard 1947)
<i>rudis</i> (Aldrich) 1916	Ne, No	S
<i>spretor</i> (Reinhard) 1947	Ne	D (Reinhard 1947)
<i>wagneri</i> (Blanchard) 1939	No	D (Blanchard 1939)

Subgenus **Lepyria** new subgenus

Three PSDC; IV setulose; explanate vesica present, Fig. 424; corpus semi-globose; with antero-ventral hooks; highly modified limen present; no juxta or copi; Figs. 422-424.

Genotype and only species *Sarcophaga melampyga* Ald. by present designation.

Its distribution is Nearctic and its biology is unknown.

Subgenus **Mecynocarpus** new subgenus

Four PSDC; IV setulose; vesica present; corpus with a midcaudal hook-like extension; limen very large, Fig. 420; anal forceps very sharply hooked, Fig. 457.

Genotype and only species *Sarcophaga salva* Ald. by present designation.

It is a Nearctic species of unknown biology.

Subgenus **Stenolaucotheca** Townsend

Stenolaucotheca Townsend 1918. Ins. Ins. Mens. 6:162. Genotype *Sarcophaga spatulata* Ald.

IV bare; explanate vesica present; limen, Fig. 414, appearing as vertical rectangle with hook below; no juxta or copi; corpus long; Figs. 413-415.

The genotype above is the only included species. It is Nearctic and probably parasitic.

Subgenus **Tephromyiella** Townsend

Tephromyiella Townsend 1917c. Ins. Ins. Mens. 5:164. Genotype *Sarcophaga atlanis* Ald.

IV bare; vesica small; large scoop-like juxta present, Fig. 416; limen large and well developed; no copi; see Figs. 416-418.

The species of this subgenus are found in the Nearctic and Palearctic regions and are parasitic, mostly on Orthoptera.

Included Species

<i>atlanis</i> (Aldrich) 1916	Ne	S
<i>arenicola</i> (Rohdendorf) 1928a	P	D (Rohdendorf 1928a)
<i>devulsa</i> (Reinhard) 1947	Ne	T (Reinhard 1947)

VII. Abbreviations Used in Text and Plates

A—Sternal arms.	LP—Lateral plate.
AC—Anterior clasper.	MC—Membranocorpus.
AF—Anal forceps.	MDP—Median dorsal projection.
AJ—Anterior juxtal process.	MF—Median filament.
AP—Anal plate.	MP—Median process.
B—Sternal base.	MM—Median marginals.
C—Corpus.	PC—Posterior claspers.
CA—Capitis.	PH—Phallus.
CO—Copi.	PHO—Phallophore.
CU—Cunabula.	PSDC—Posterior dorsocentrals.
DR—Dorsal rods.	PT—Phallic tube.
H—Harpes.	SC—Sclerocorpus.
HI—Hillae.	ST—Stemmatitis.
J—Juxta.	V—Vesica.
L—Limen.	VS—Ventral sclerotization.
LA—Lateral arms.	W—Sternal window.
LDP—Lateral dorsal projection.	2A-7A—Abdominal segments.
LF—Lateral filament.	2S-6S—Abdominal sternites.
LJ—Lateral juxtal process.	1V-5V—Wing veins.

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PLATES WITH EXPLANATIONS

PLATE 1

FIG. 1. Hypothetical sarcophagine aedeagus, lateral view.

Scopeuma stercorarium (Linnaeus)

FIG. 2. Fifth sternite.

FIG. 3. Aedeagus, lateral view.

FIG. 4. Phallus, antero-dorsal view.

FIG. 5. Anal plate and forceps, lateral view.

Spathiophora cincta Loew

FIG. 6. Fifth sternite.

FIG. 7. Aedeagus, lateral view.

FIG. 8. Phallus, anterior view.

Senotainia trilineata, var *argentifrons* Townsend

FIG. 9. Aedeagus, lateral view.

Agria affinis (Fallén)

FIG. 10. Fifth sternite.

FIG. 11. Phallus, ventral view—phallic tube omitted.

FIG. 12. Phallus, anterior view.

FIG. 13. Phallus, lateral view.

PLATE I

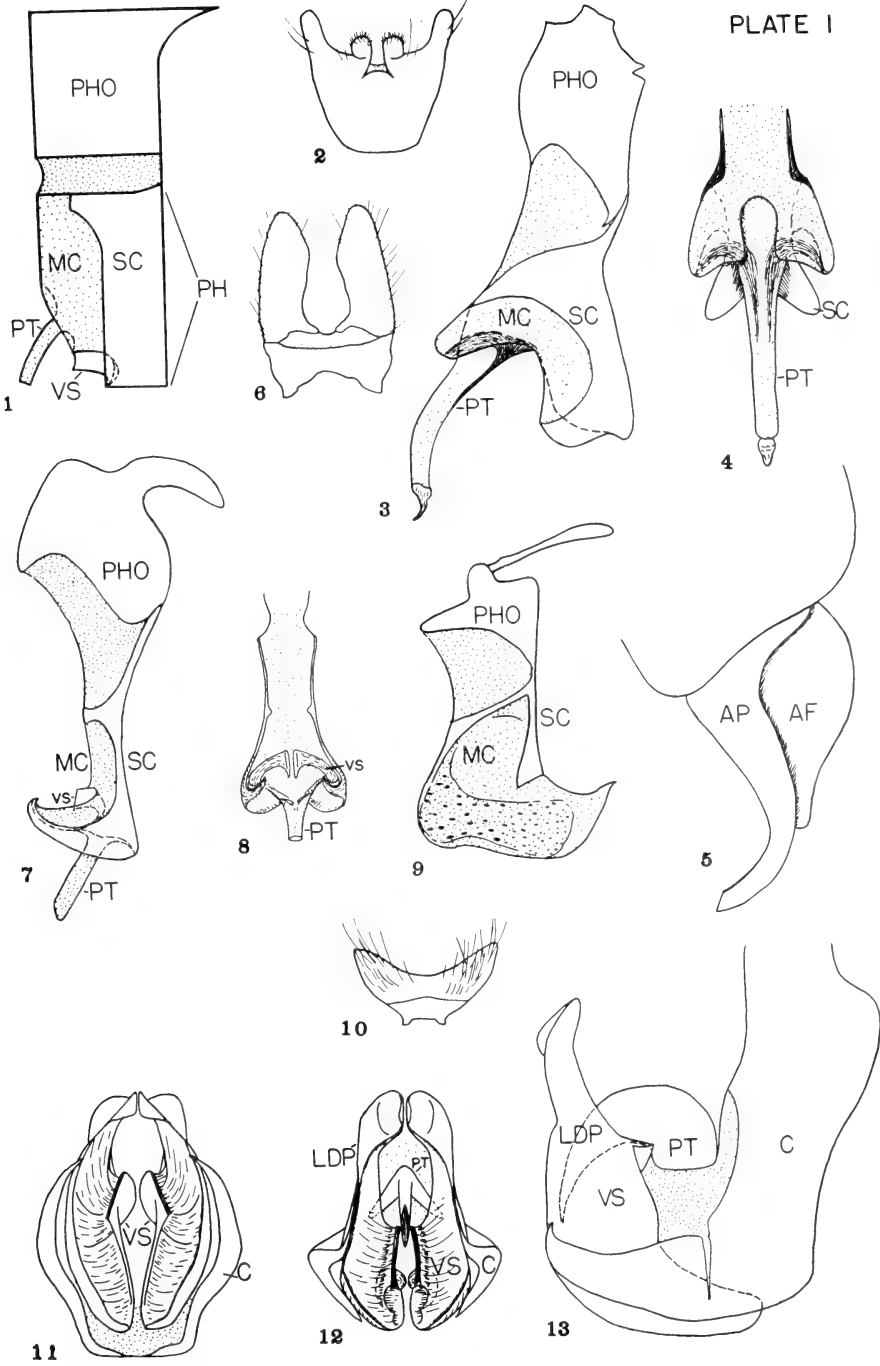


PLATE 2

Sarcofahrtia ravinia Parker

- FIG. 14. Phallus, lateral view.
FIG. 15. Phallus, anterior view.
FIG. 16. Fifth sternite.

Wohlfahrtia vigil (Walker)

- FIG. 17. Fifth sternite.
FIG. 18. Tip of phallus, anterior view.
FIG. 19. Phallus, lateral view.

Imparia impar (Aldrich)

- FIG. 20. Phallus, anterior view.
FIG. 21. Phallus, left lateral view.
FIG. 22. Phallus, right lateral view.
FIG. 23. Fifth sternite.

Sarcophagula femoralis (Schiner)

- FIG. 24. Fifth sternite.
FIG. 25. Aedeagus, lateral view.
FIG. 26. Lateral arms and median process, caudo-ventral view.
FIG. 27. Tip of phallus, anterior view.

Sarcophagula occidua (Fabricius)

- FIG. 28. Fifth sternite.
FIG. 29. Aedeagus, lateral view.

PLATE 2

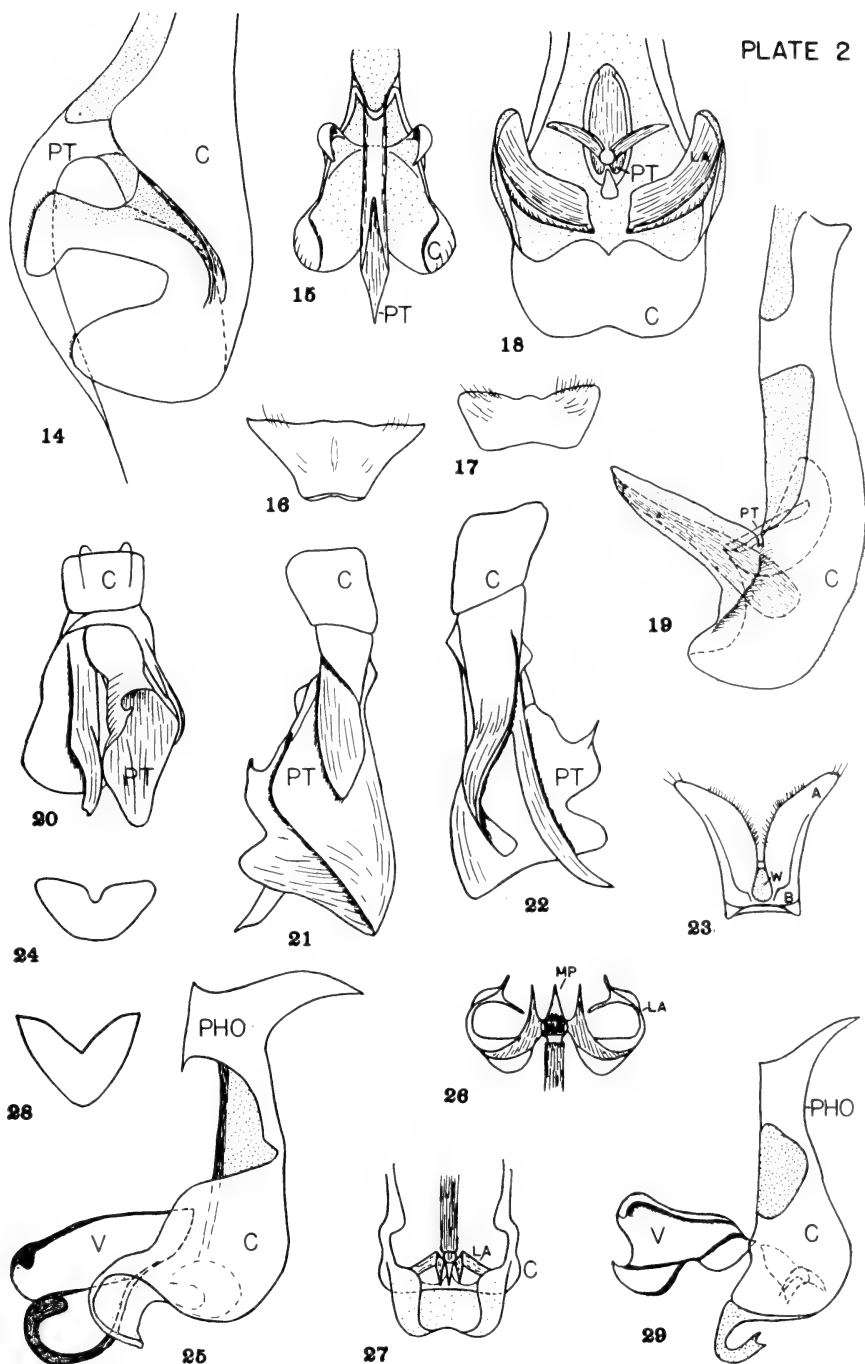


PLATE 3

Hypopelta scrofa Aldrich

FIG. 30. Phallus, caudal view.

FIG. 31. Juxta and filaments, antero-dorsal view.

FIG. 32. Phallus, lateral view.

Camptops unicolor Aldrich

FIG. 33. Attachment of right lateral filament to corpus, mesodorsal view.

FIG. 34. Phallus, anterior view.

FIG. 35. Fifth sternite.

FIG. 36. Phallus, lateral view.

Argoravinia modesta (Wiedemann)

FIG. 37. Fifth sternite.

FIG. 38. Phallus, caudal view.

FIG. 39. Phallus, lateral view.

Chloronesia sp.

FIG. 40. Juxta, ventral view.

FIG. 41. Phallus, lateral view.

FIG. 42. Fifth sternite.

Johnsonia (*Johnsonia*) sp.

FIG. 43. Fifth sternite.

FIG. 44. Phallus, lateral view.

PLATE 3

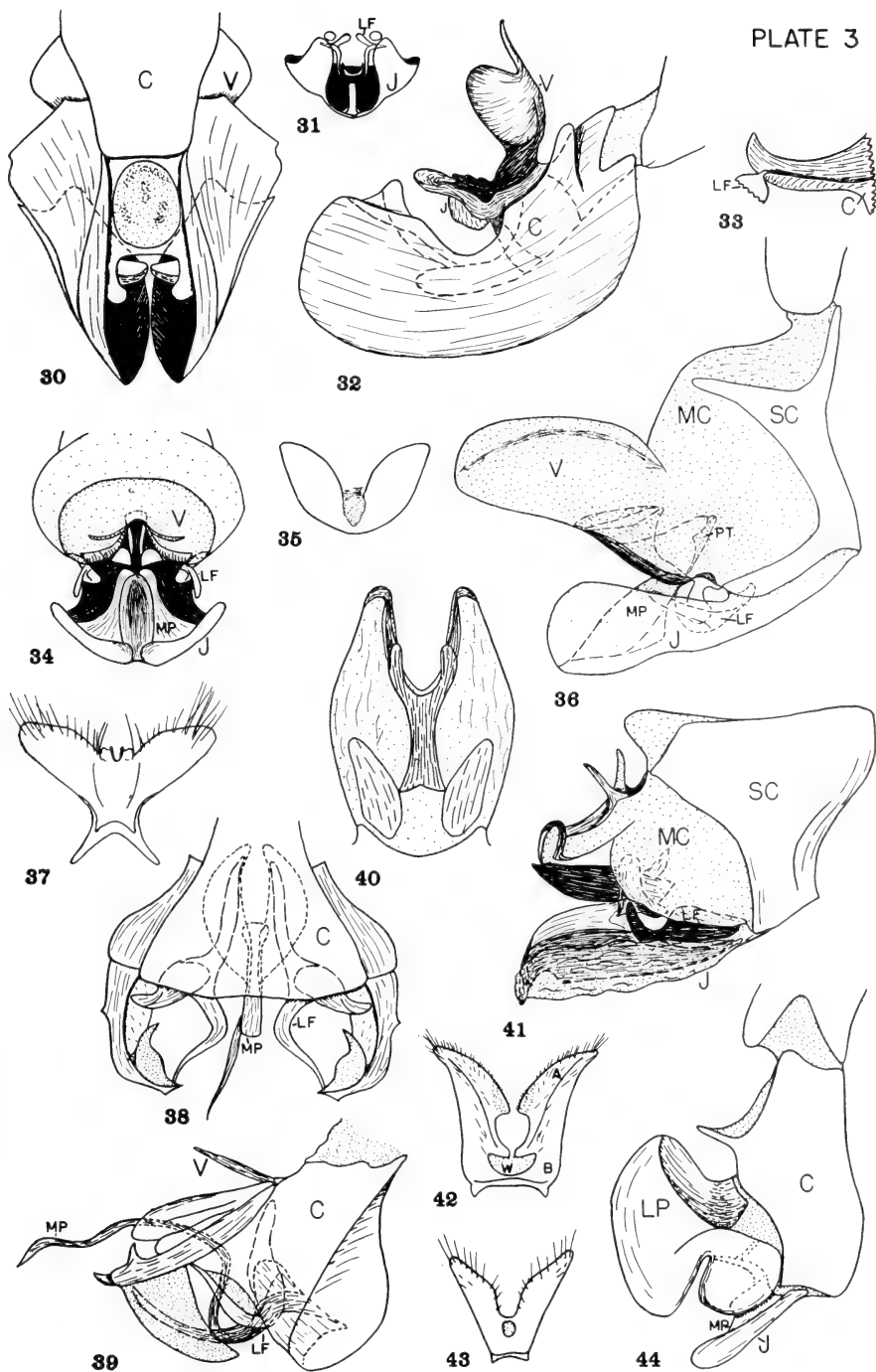


PLATE 4

Johnsonia (Emblemasoma) erro (Aldrich)

- FIG. 45. Phallus, lateral view.
FIG. 46. Phallus, anterior view.
FIG. 47. Fifth sternite.

Johnsonia (Johnsonia) rufitibia (Van der Wulp)

- FIG. 48. Phallus, lateral view.
FIG. 49. Phallus, anterior view.
FIG. 50. Juxta, ventral view.
FIG. 51. Fifth sternite.

Helicobia morionella (Aldrich)

- FIG. 52. Phallus, lateral view.
FIG. 53. Fifth sternite.
FIG. 54. Juxta, median process and capitis, lateral view.
FIG. 55. Juxta, ventral view.
FIG. 56. Right lateral filament, lateral view.

Helicobia rapax (Walker)

- FIG. 57. Juxta, ventral view.
FIG. 58. Aedeagus, lateral view.
FIG. 59. Phallus, lateral view—lateral plates removed.
FIG. 60. Fifth sternite.

Helicobia stellata (Van der Wulp)

- FIG. 61. Juxta, ventral view.
FIG. 62. Phallus, lateral view.

PLATE 4

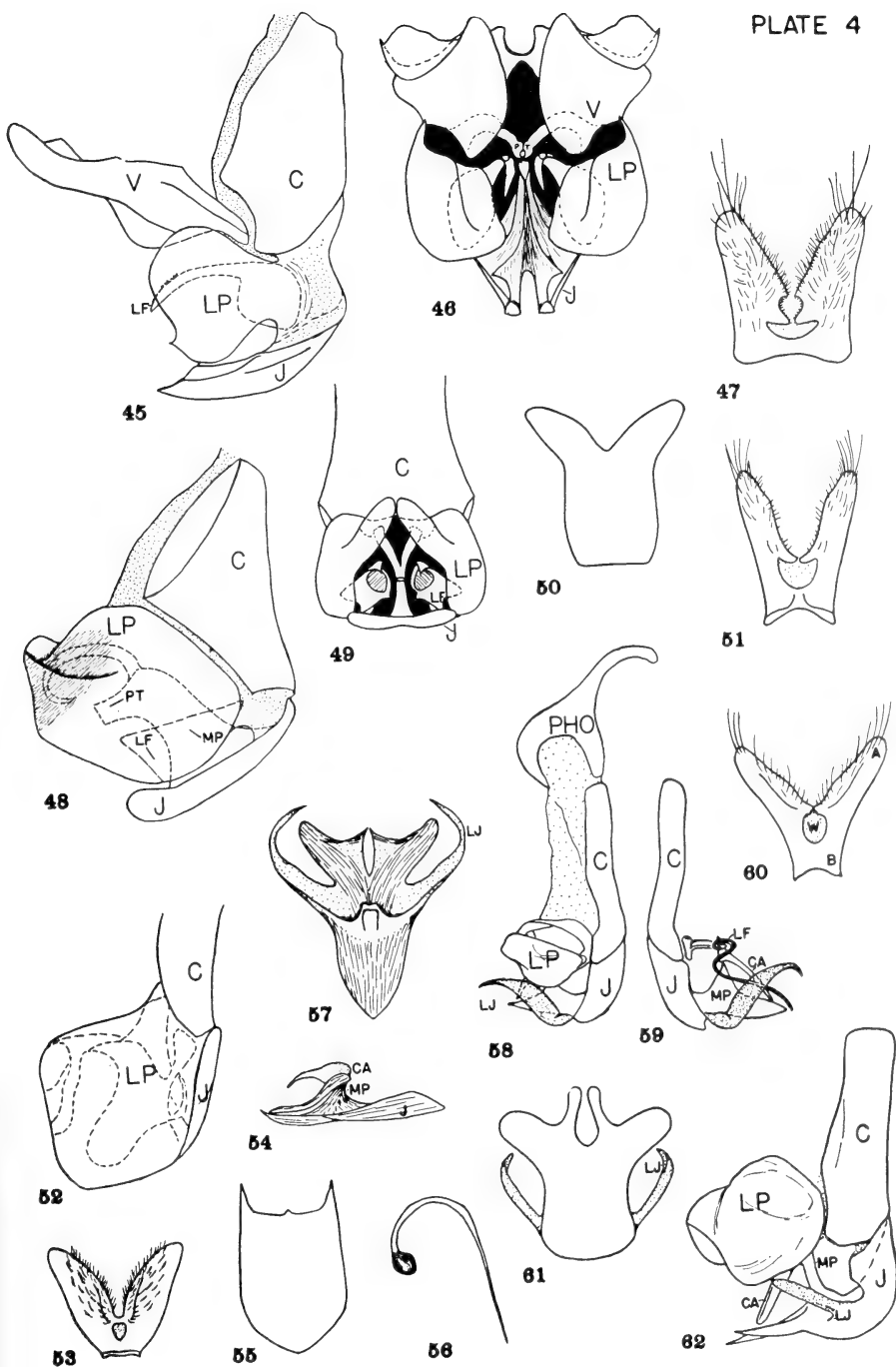


PLATE 5

Helicobia australis Johnston & Tiegs

FIG. 63. Phallus, lateral view.

FIG. 64. Juxta, median process and capitis, lateral view.

FIG. 65. Fifth sternite.

FIG. 66. Corpus, anterior view.

Arachnidomyia hinei (Aldrich)

FIG. 67. Fifth sternite.

FIG. 68. Phallus, lateral view.

FIG. 69. Juxta, median process and capitis, lateral view.

Arachnidomyia davidsoni (Coquillett)

FIG. 70. Juxta, median process and capitis, lateral view.

FIG. 71. Fifth sternite.

FIG. 72. Phallus, lateral view.

Arachnidomyia houghi (Aldrich)

FIG. 73. Juxta, median process and capitis, lateral view.

FIG. 74. Left lateral filament, anterior view.

FIG. 75. Phallus, lateral view.

PLATE 5

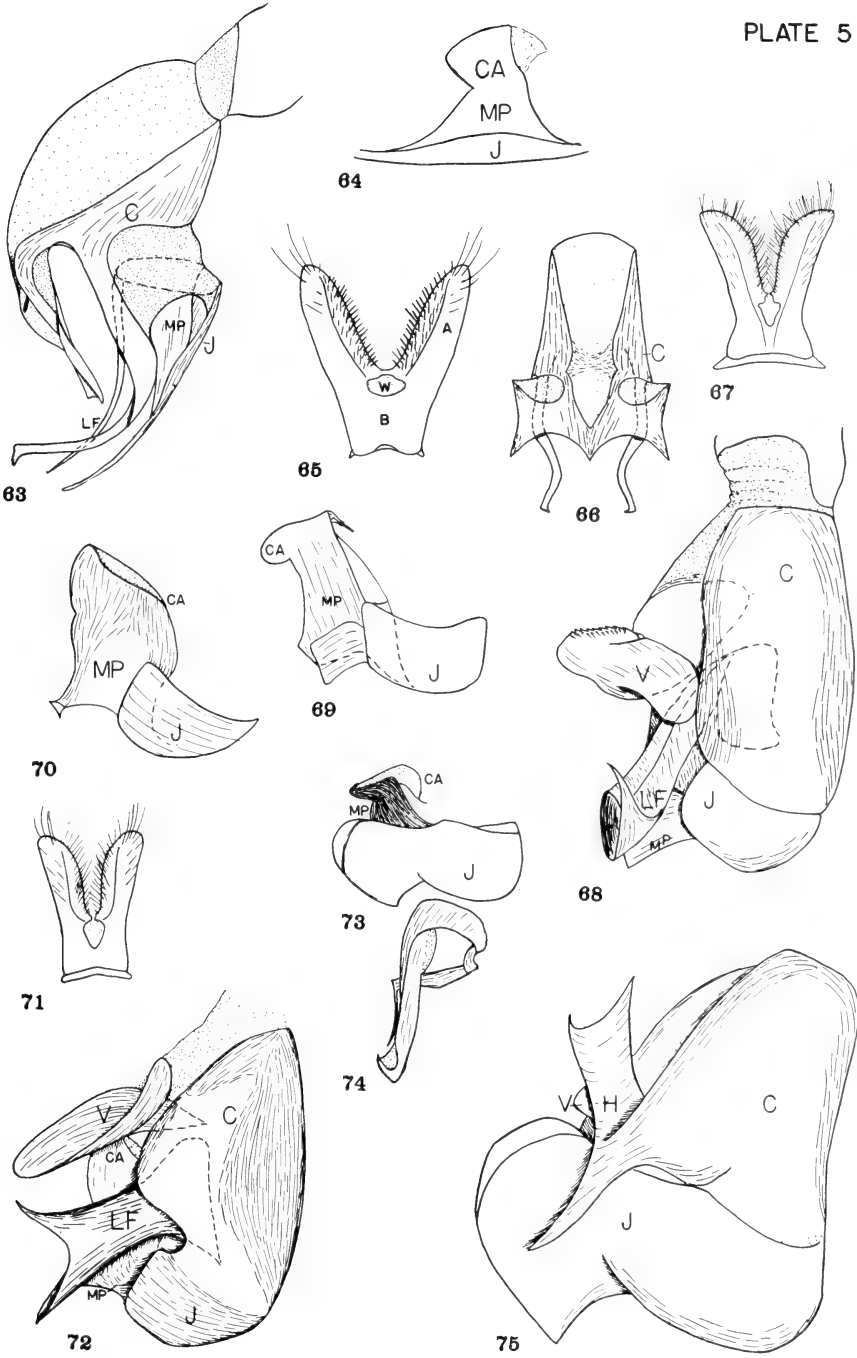


PLATE 6

Arachnidomyia aldrichi (Parker)

FIG. 76. Phallus, lateral view.

FIG. 77. Juxta, median process and capitis, lateral view.

FIG. 78. Left lateral filament, anterior view.

Sarcomyia scelestia (Hall)

FIG. 79. Phallus, lateral view.

FIG. 80. Phallus, anterior view.

FIG. 81. Fifth sternite.

Wohlfahrtiopsis johnsoni (Aldrich)

FIG. 82. Phallus, lateral view.

FIG. 83. Fifth sternite.

FIG. 84. Lateral filaments and capitis, dorsal view.

Wohlfahrtiopsis bishoppi (Aldrich)

FIG. 85. Fifth sternite.

FIG. 86. Phallus, lateral view.

Wohlfahrtiopsis utilis (Aldrich)

FIG. 87. Juxta, median process and capitis, lateral view.

FIG. 88. Fifth sternite.

FIG. 89. Phallus, lateral view.

PLATE 6

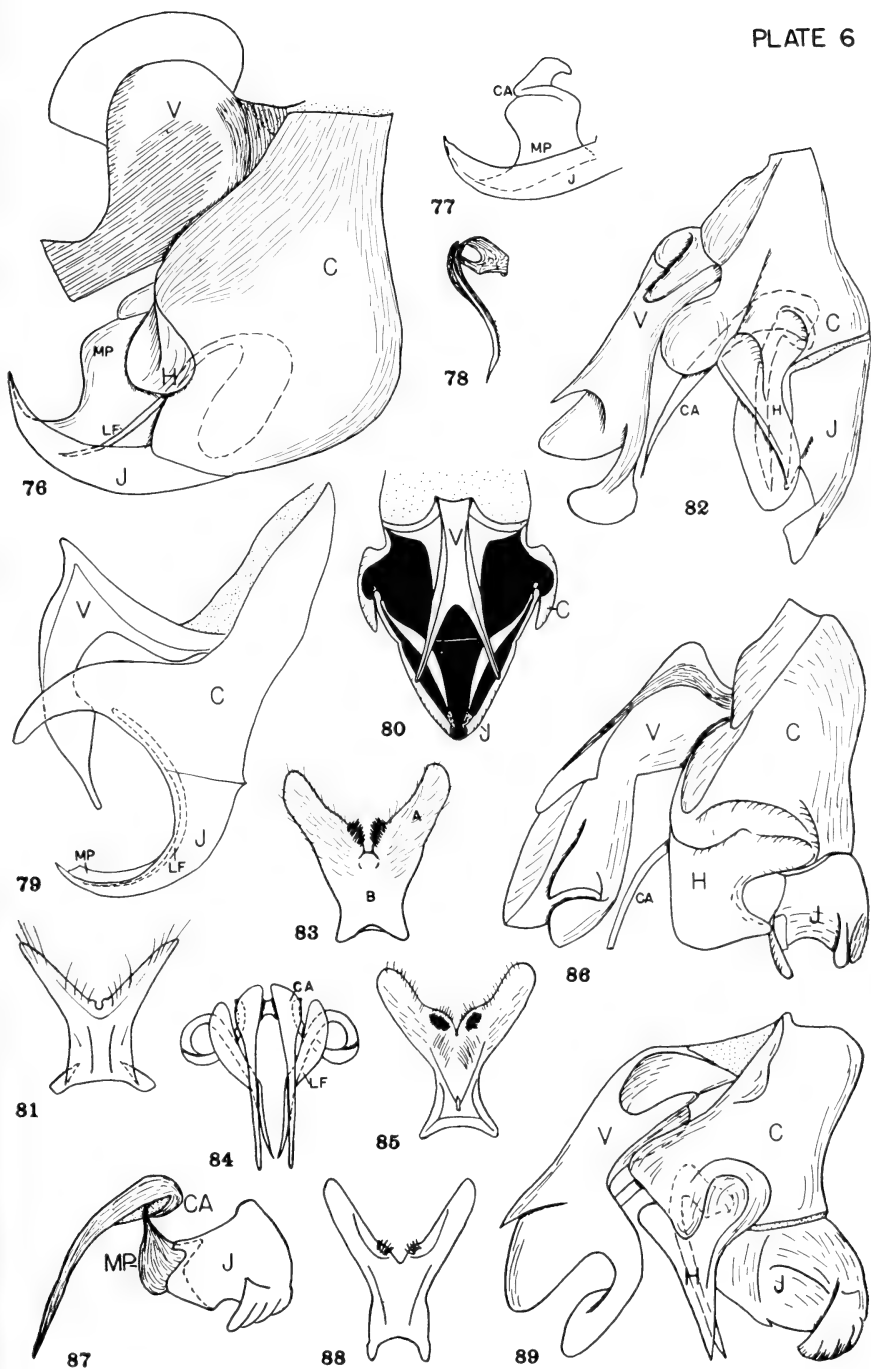


PLATE 7

Sapromyia polistensis (Hall)

FIG. 90. Phallus, lateral view.

FIG. 91. Fifth sternite.

FIG. 92. Capitis and median process, lateral view.

Sapromyia cooleyi (Parker)

FIG. 93. Phallus, lateral view.

FIG. 94. Left lateral filament, anterior view.

FIG. 95. Fifth sternite.

FIG. 96. Juxta, ventral view.

FIG. 97. Vesica, anterior view.

FIG. 98. Juxta, median process and capitis, lateral view.

Sapromyia bullata (Parker)

FIG. 99. Phallus, lateral view.

FIG. 100. Juxta, ventral view.

FIG. 101. Fifth sternite.

FIG. 102. Juxta, median process and capitis, lateral view.

Sarcophaga melanura Meigen

FIG. 103. Fifth sternite.

FIG. 104. Phallus, lateral view.

FIG. 105. Phallus, anterior view.

Sarcophaga sinuata Meigen

FIG. 106. Left lateral filament, antero-mesal view.

FIG. 107. Fifth sternite.

FIG. 108. Juxta and median process, lateral view.

FIG. 109. Phallus, lateral view.

PLATE 7

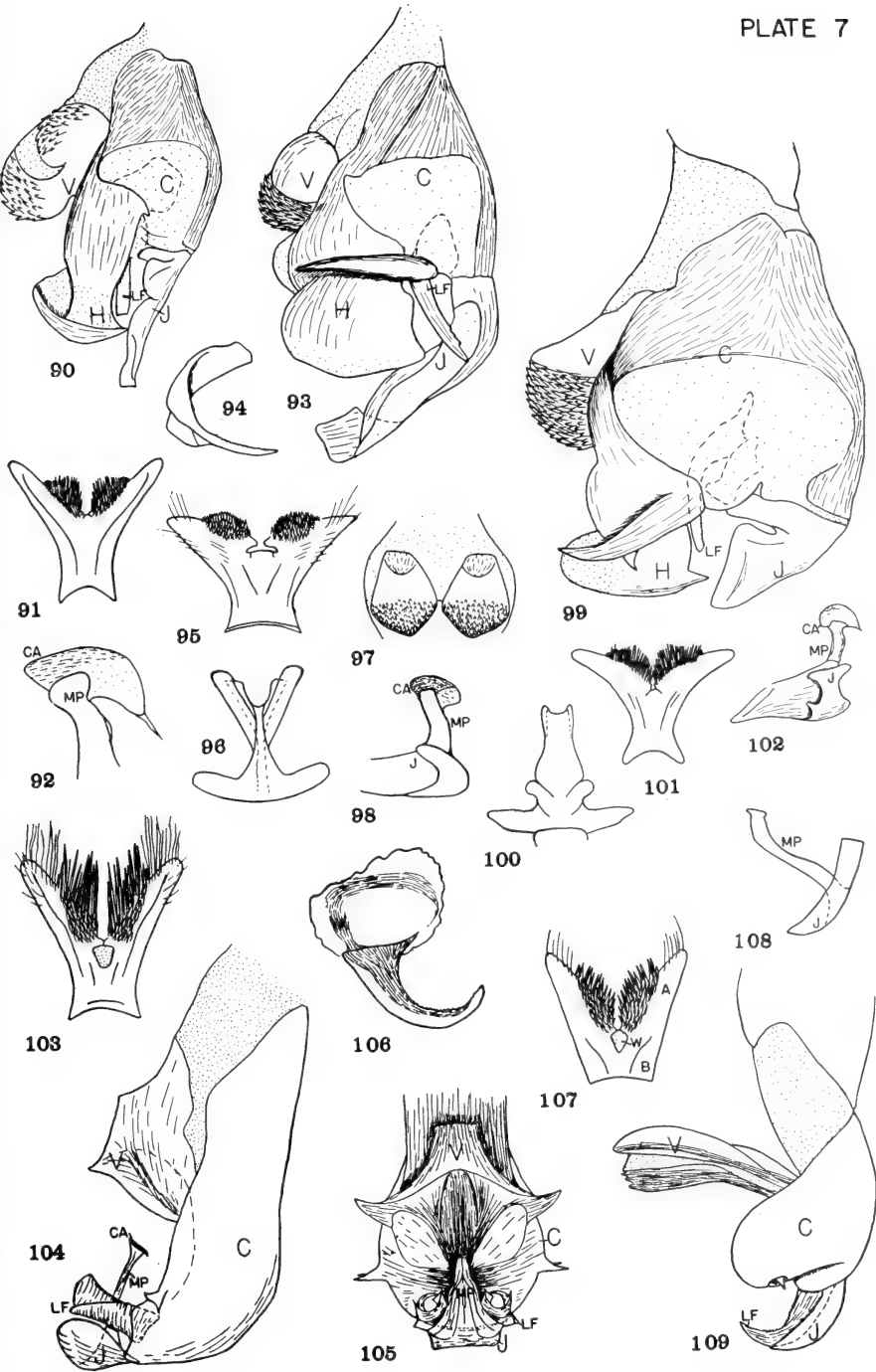


PLATE 8

Sarcophaga vagans Meigen

FIG. 110. Phallus, lateral view.

FIG. 111. Fifth sternite.

Sarcophaga offuscata Meigen

FIG. 112. Phallus, lateral view.

Sarcophaga haemorrhoea Meigen

FIG. 113. Phallus, lateral view.

FIG. 114. Fifth sternite.

FIG. 115. Phallus, anterior view.

Sarcophaga cucullans Pandellé

FIG. 116. Fifth sternite.

FIG. 117. Phallus, lateral view.

FIG. 118. Juxta, lateral juxtal process, median process and capitis, lateral view.

Sarcophaga pumila Meigen

FIG. 119. Phallus, anterior view.

FIG. 120. Phallus, lateral view.

FIG. 121. Capitis and median process, lateral view.

FIG. 122. Fifth sternite.

Sarcophaga arcipes Pandellé

FIG. 123. Fifth sternite.

FIG. 124. Phallus, lateral view.

PLATE 8

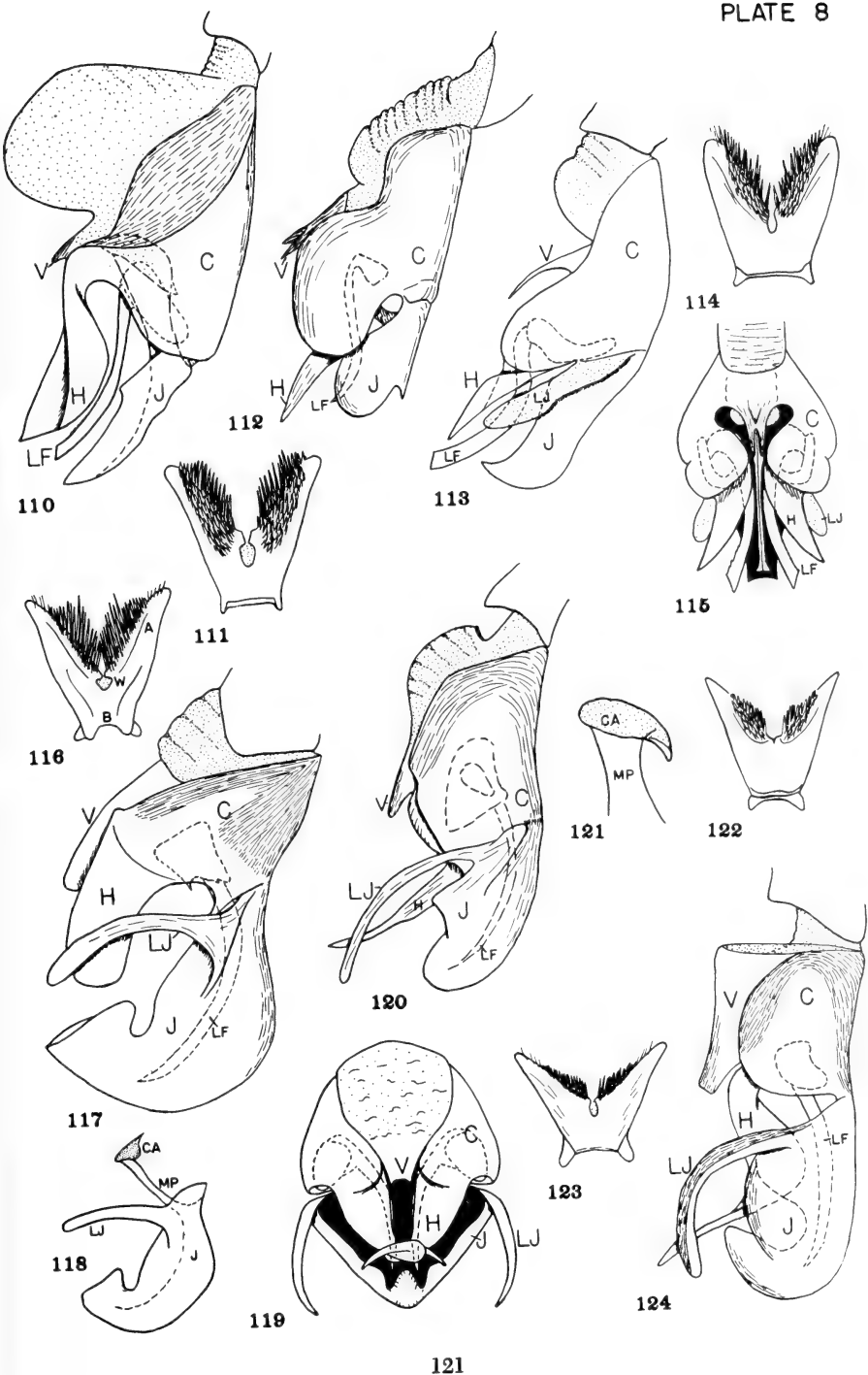


PLATE 9

Sarcophaga exuberans Pandellé

FIG. 125. Phallus, lateral view.

FIG. 126. Fifth sternite.

Sarcophaga misera Walker

FIG. 127. Fifth sternite.

FIG. 128. Phallus, lateral view.

FIG. 129. Juxta and lateral juxtal processes, caudo-ventral view.

Sarcophaga sarracenioides Aldrich

FIG. 130. Right lateral filament, caudal view.

FIG. 131. Phallus, lateral view.

FIG. 132. Fifth sternite.

FIG. 133. Juxta, lateral juxtal process, median process and capitis, lateral view.

FIG. 134. Vesica, dorsal view.

Sarcophaga harpax Pandellé

FIG. 135. Phallus, lateral view.

Sarcophaga scoparia var *nearctica* Parker

FIG. 136. Fifth sternite.

FIG. 137. Right lateral filament, anterior view.

FIG. 138. Phallus, lateral view.

FIG. 139. Juxta, median process and capitis, lateral view.

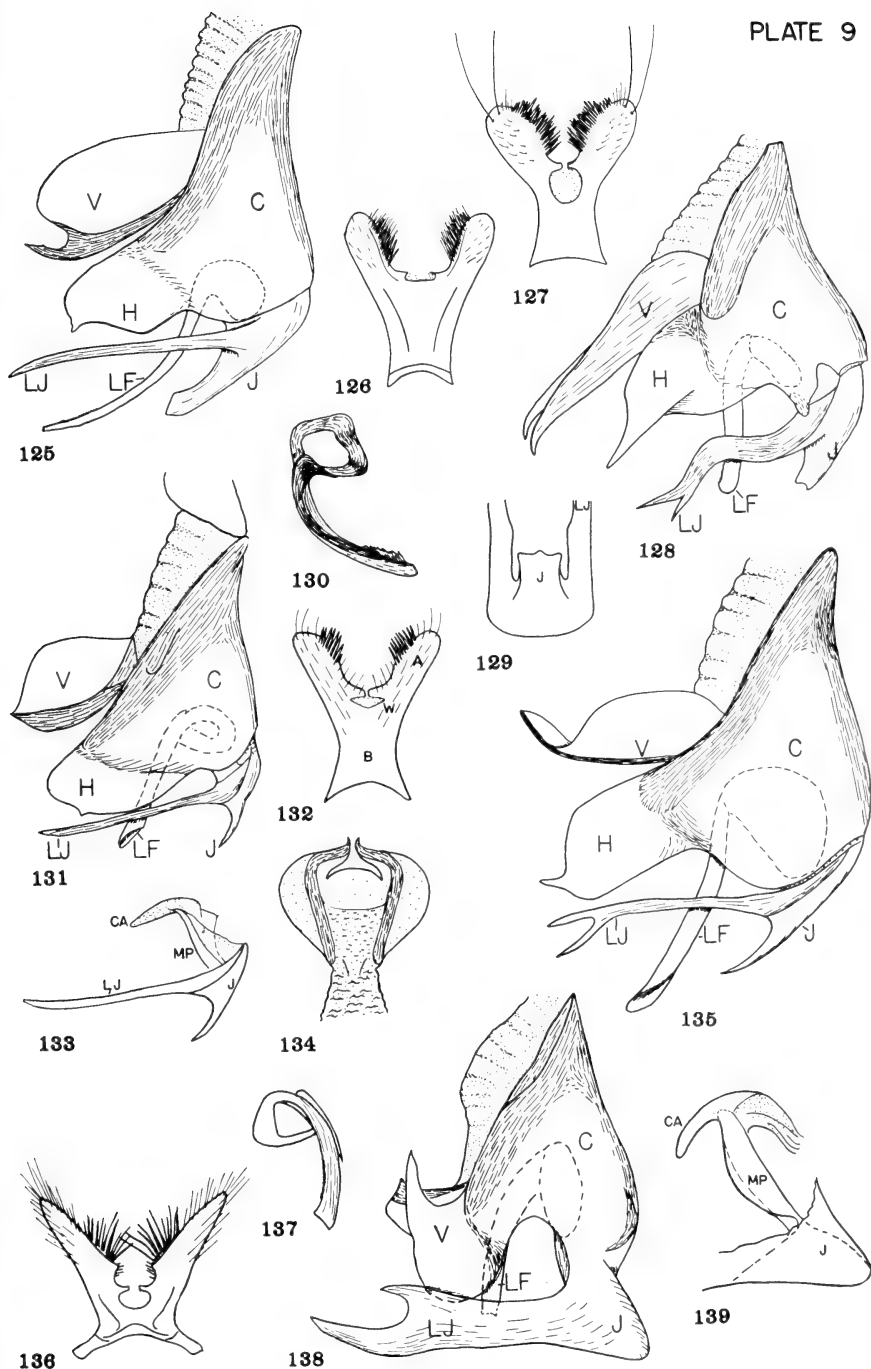


PLATE 10

Sarcophaga argyrostoma Robineau-Desvoidy

FIG. 140. Phallus, lateral view.

FIG. 141. Juxta, lateral juxtal process, median process and capitis, lateral view.

FIG. 142. Fifth sternite.

Sarcophaga crassipalpis Macquart

FIG. 143. Phallus, antero-dorsal view.

FIG. 144. Fifth sternite.

FIG. 145. Phallus, lateral view.

FIG. 146. Juxta, lateral juxtal process, median process and capitis, lateral view.

Sarcophaga protuberans Pandellé

FIG. 147. Capitis and median process, lateral view.

FIG. 148. Phallus, lateral view.

FIG. 149. Fifth sternite, base missing.

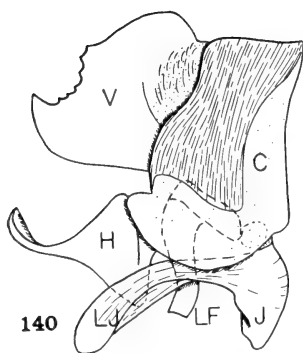
Sarcophaga privigna Rondani

FIG. 150. Fifth sternite.

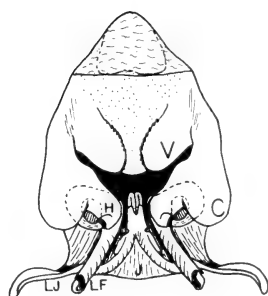
FIG. 151. Capitis and median process, lateral view.

FIG. 152. Phallus, lateral view.

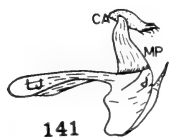
PLATE 10



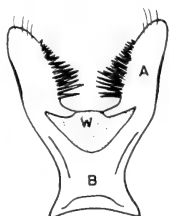
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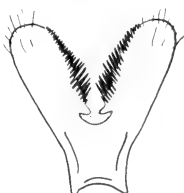
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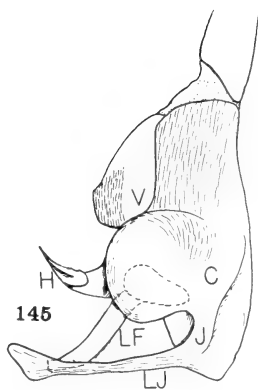
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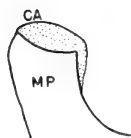
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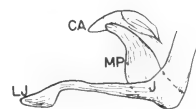
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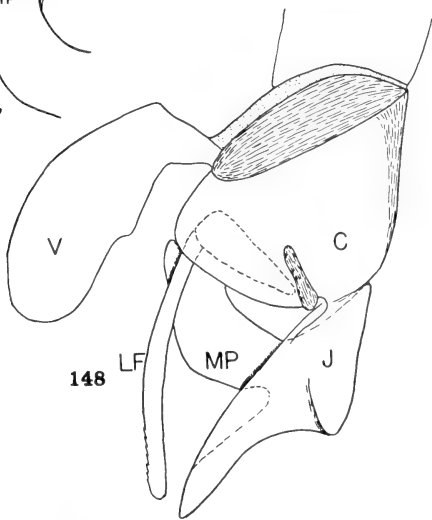
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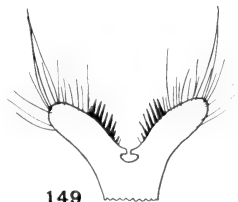
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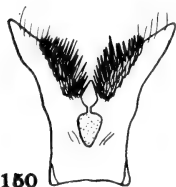
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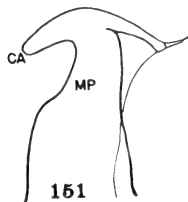
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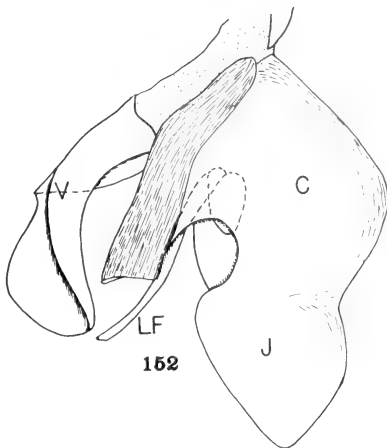
149



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151



152

PLATE 11

Sarcophaga aratrix Pandellé

FIG. 153. Phallus, lateral view.

FIG. 154. Fifth sternite.

FIG. 155. Capitis and median process, lateral view.

Sarcophaga idonea Aldrich

FIG. 156. Capitis, lateral view.

FIG. 157. Harpes, anterior view.

FIG. 158. Phallus, lateral view.

FIG. 159. Fifth sternite.

Sarcophaga sima Aldrich

FIG. 160. Juxta, median process and capitis, lateral view.

FIG. 161. Phallus, lateral view.

FIG. 162. Fifth sternite.

Sarcophaga tarsata Aldrich

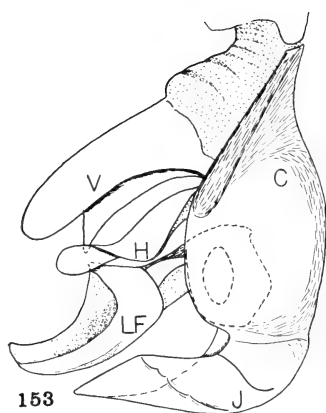
FIG. 163. Juxta, median process and capitis, lateral view.

FIG. 164. Left lateral filament, anterior view.

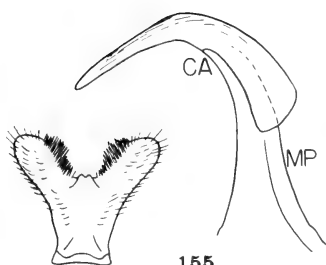
FIG. 165. Phallus, anterior view, vesica removed.

FIG. 166. Fifth sternite.

FIG. 167. Phallus, lateral view.

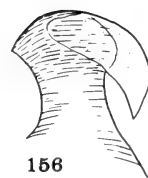


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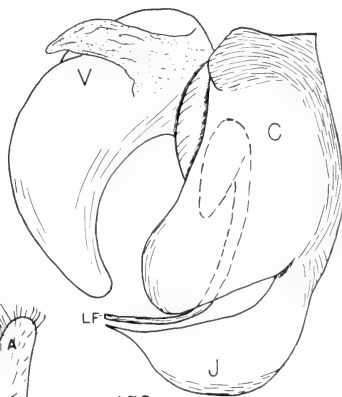
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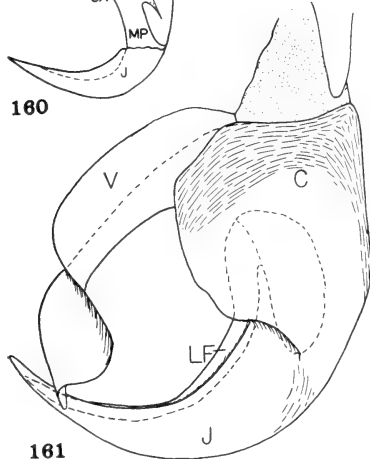
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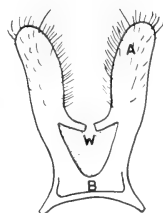
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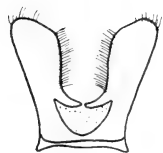
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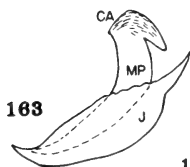
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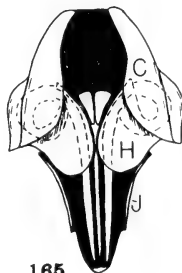
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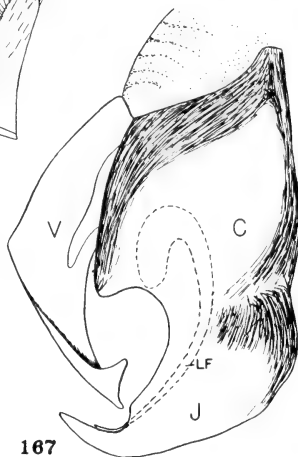
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165



167

PLATE 12

Sarcophaga parallela Aldrich

FIG. 168. Juxta, median process and capitis, lateral view.

FIG. 169. Phallus, lateral view.

FIG. 170. Fifth sternite.

Sarcophaga sarraceniae Riley

FIG. 171. Fifth sternite.

FIG. 172. Capitis, lateral view.

FIG. 173. Phallus, lateral view.

Sarcophaga soror Rondani

FIG. 174. Phallus, lateral view.

FIG. 175. Harpes, anterior view.

Sarcophaga tetra Aldrich

FIG. 176. Fifth sternite.

FIG. 177. Phallus, lateral view.

FIG. 178. Phallus, anterior view.

Sarcophaga nigriventris Meigen

FIG. 178. 1. Fifth sternite.

FIG. 178. 2. Phallus, lateral view.

FIG. 178. 3. Phallus, anterior view—vesica removed.

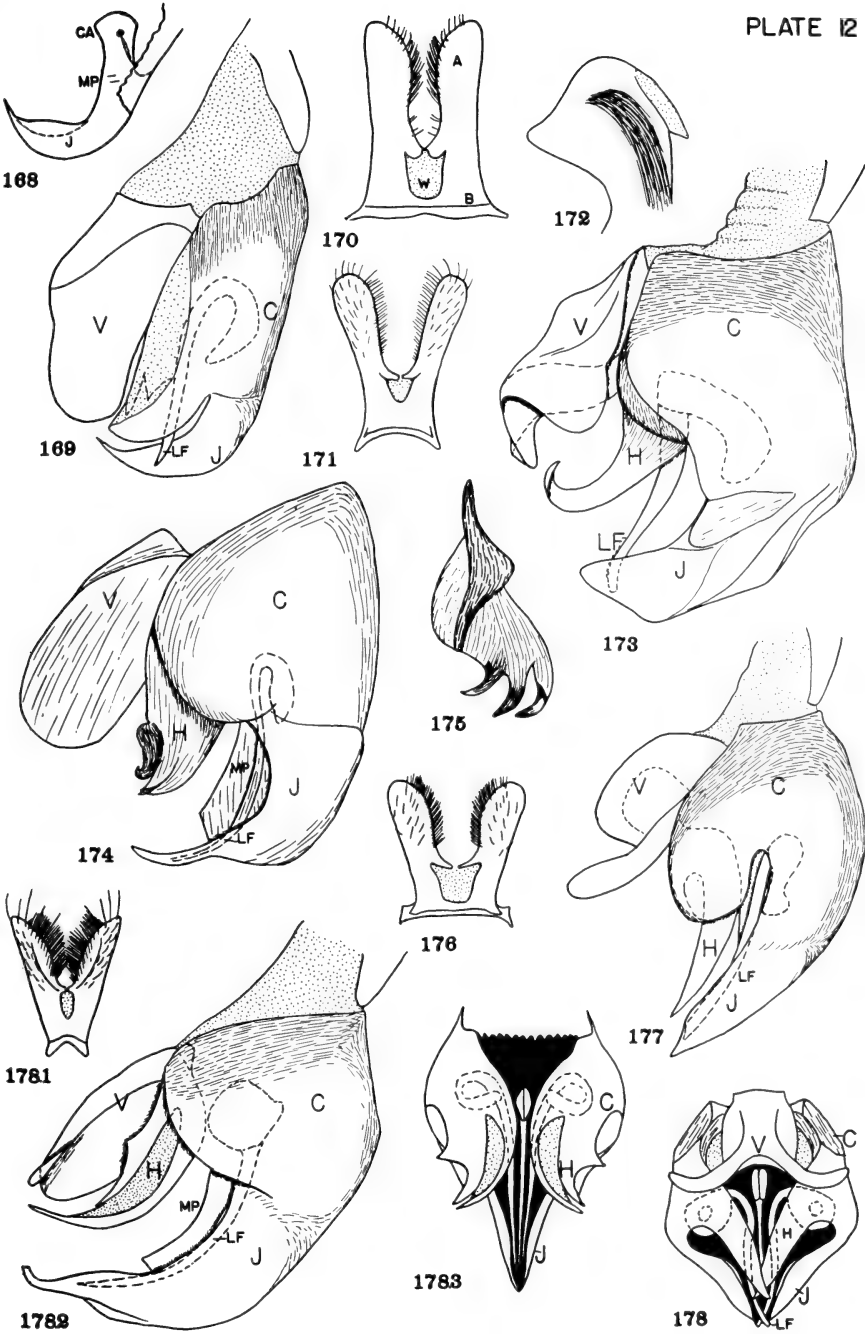


PLATE 13

Sarcophaga incisilobata Pandellé

FIG. 179. Phallus, lateral view.

FIG. 180. Juxta, ventral view.

FIG. 181. Fifth sternite.

Sarcophaga pulla Aldrich

FIG. 182. Fifth sternite.

FIG. 183. Phallus, lateral view.

FIG. 184. Capitis and median process, lateral view.

FIG. 185. Harpes, anterior view.

Sarcophaga occidentalis Aldrich

FIG. 186. Phallus, anterior view.

FIG. 187. Juxta, median process and capitis, lateral view.

FIG. 188. Left lateral filament, antero-lateral view.

FIG. 189. Harpes, anterior view.

FIG. 190. Fifth sternite.

Sarcophaga fulvipes Macquart

FIG. 191. Phallus, lateral view.

FIG. 192. Left lateral filament, ventral view.

FIG. 193. Fifth sternite.

FIG. 194. Capitis and median process, lateral view.

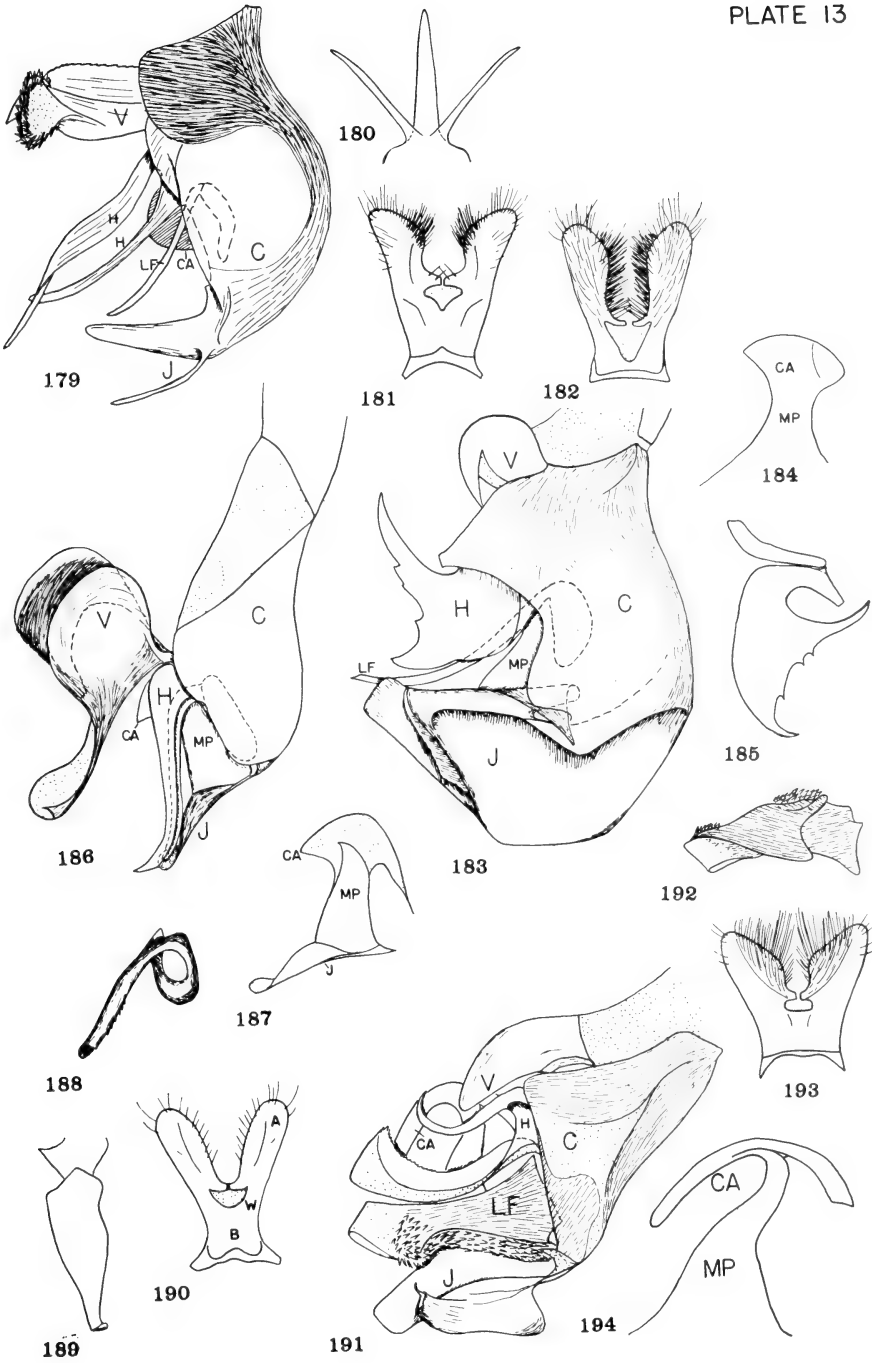


PLATE 14

Sarcophaga carnaria (Linnaeus)

- FIG. 195. Phallus, lateral view.
FIG. 196. Juxta of another specimen.
FIG. 197. Left lateral filament, meso-ventral view.
FIG. 198. Juxta, median process and capitis, lateral view.
FIG. 199. Phallus, anterior view—vesica removed.
FIG. 200. Fifth sternite.

Sarcophaga thatuna Aldrich

- FIG. 201. Phallus, lateral view.
FIG. 202. Fifth sternite.

Sarcophaga juliaetta Aldrich

- FIG. 203. Phallus, lateral view.
FIG. 204. Fifth sternite.

Sarcophaga gracilis Aldrich

- FIG. 205. Fifth sternite.
FIG. 206. Vesica, dorsal view.
FIG. 207. Juxta, median process and capitis, lateral view.
FIG. 208. Phallus, lateral view.

PLATE 14

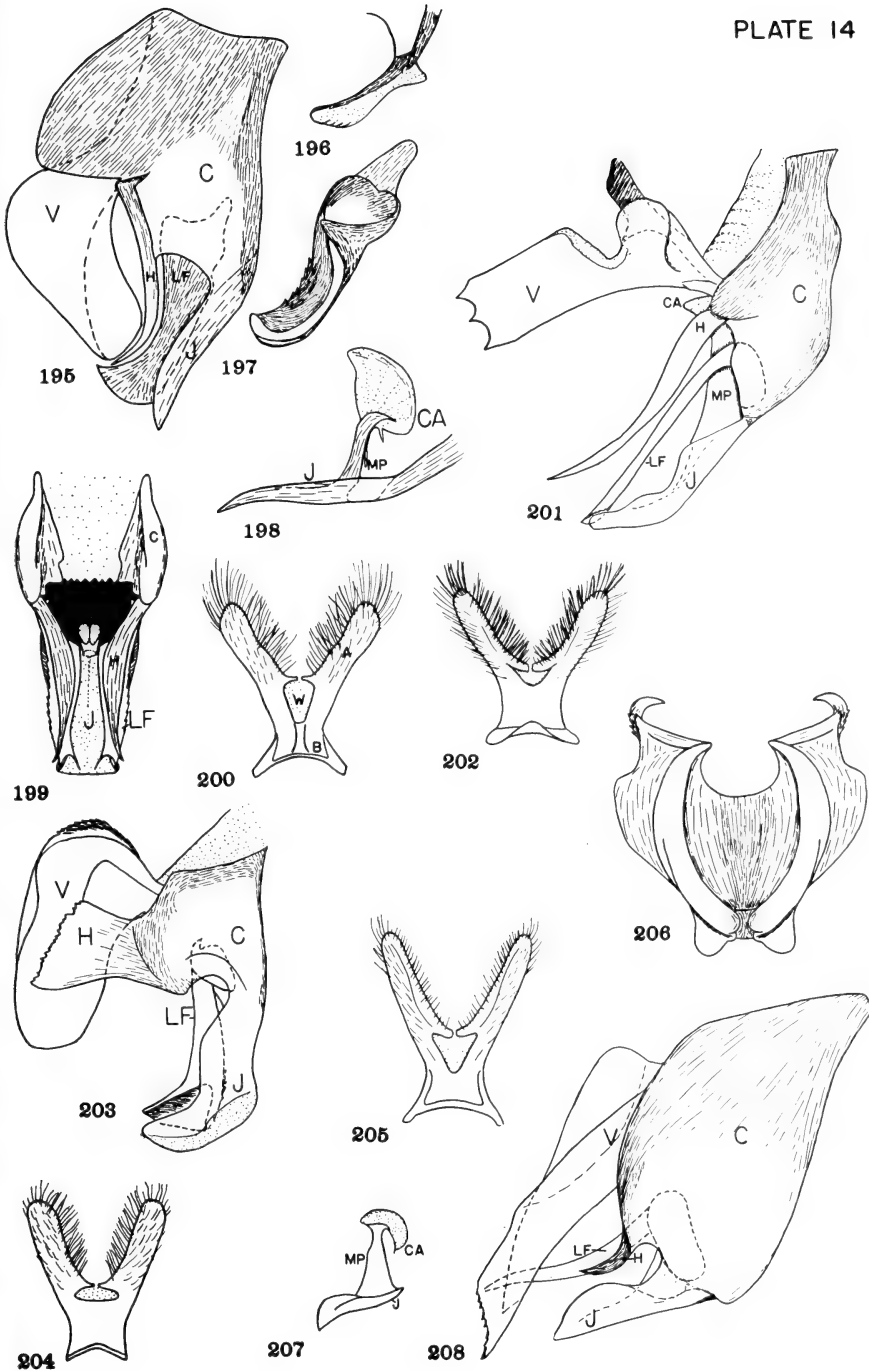


PLATE 15

Sarcophaga haemorrhoidalis (Fallén)

- FIG. 209. Tip of phallus, lateral view.
FIG. 210. Tip of phallus, anterior view.
FIG. 211. Juxta, median process and capitis, lateral view.
FIG. 212. Fifth sternite.

Sarcophaga piva Roback

- FIG. 213. Phallus, lateral view.
FIG. 214. Fifth sternite.

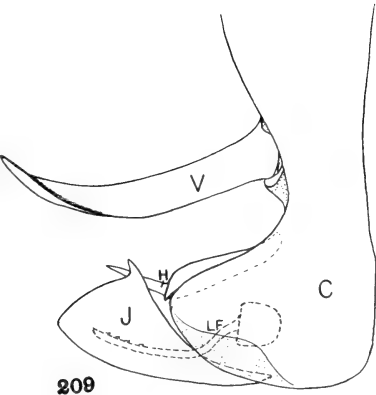
Ravinia stimulans (Walker)

- FIG. 215. Phallus, caudal view.
FIG. 216. Median process and dorsal rod, antero-lateral view.
FIG. 217. Phallus, lateral view.
FIG. 218. Fifth sternite.
FIG. 219. Phallus, anterior view—hilae removed.

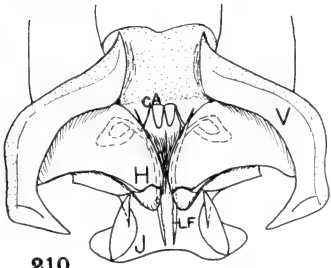
Ravinia laakei (Hall)

- FIG. 220. Phallus, lateral view.
FIG. 221. Vesica, dorsal view.
FIG. 222. Median process and dorsal rod, antero-lateral view.
FIG. 223. Median process, antero-dorsal view.
FIG. 224. Fifth sternite.

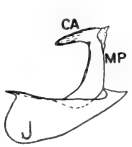
PLATE 15



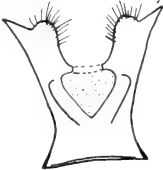
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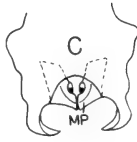
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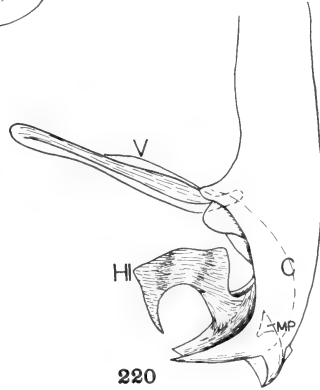
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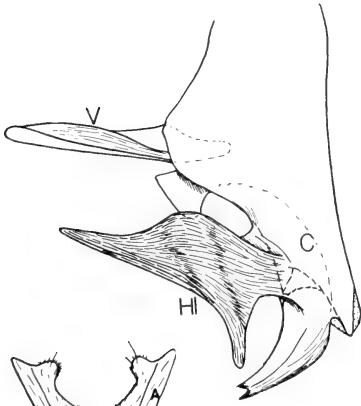
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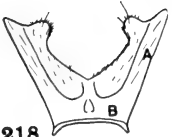
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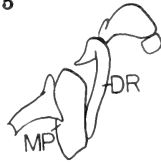
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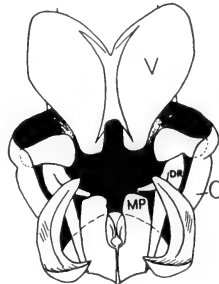
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224

PLATE 16

Ravinia latisetosa Parker

FIG. 225. Fifth sternite.

FIG. 226. Phallus, lateral view.

Ravinia effrenata (Walker)

FIG. 227. Juxta and associated structures, antero-dorsal view.

FIG. 228. Fifth sternite.

FIG. 229. Phallus, lateral view.

Ravinia errabunda (Van der Wulp)

FIG. 230. Fifth sternite.

FIG. 231. Phallus, lateral view.

FIG. 232. Internal structures of phallus, anterior view—vesica and most of corpus removed.

Ravinia aurigena (Townsend)

FIG. 233. Phallus, lateral view.

FIG. 234. Fifth sternite.

Ravinia floridensis (Aldrich)

FIG. 235. Fifth sternite.

FIG. 236. Phallus, lateral view.

PLATE 16

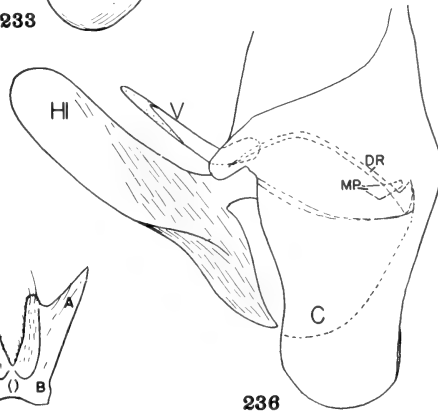
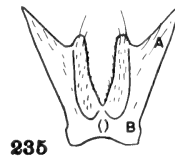
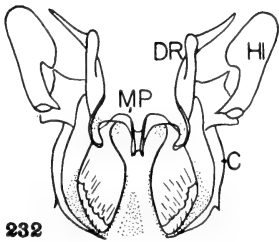
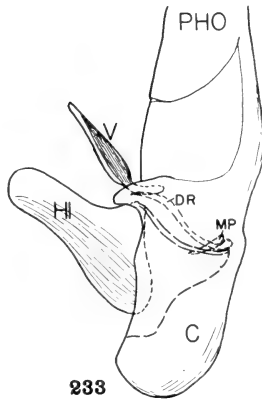
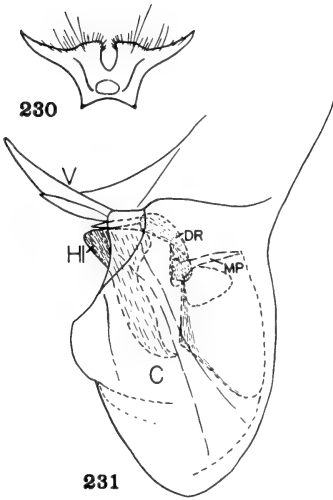
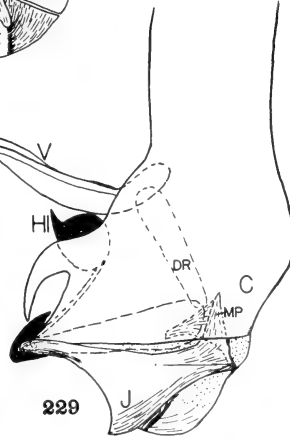
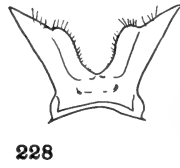
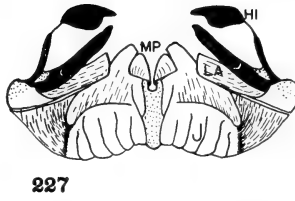
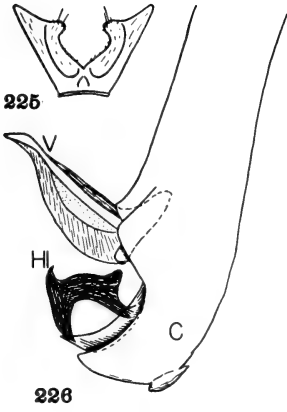


PLATE 17

Ravinia sueta (Van der Wulp)

FIG. 237. Phallus, lateral view.

FIG. 238. Dorsal rod, median process, lateral view.

FIG. 239. Fifth sternite.

Ravinia querula (Walker)

FIG. 240. Phallus, lateral view.

FIG. 241. Fifth sternite.

Ravinia l'herminieri (Robineau-Desvoidy)

FIG. 242. Fifth sternite.

FIG. 243. Phallus, lateral view.

FIG. 244. Phallus, antero-ventral view—hillae removed.

Ravinia planifrons (Aldrich)

FIG. 245. Fifth sternite.

FIG. 246. Phallus, lateral view.

Ravinia pectinata (Aldrich)

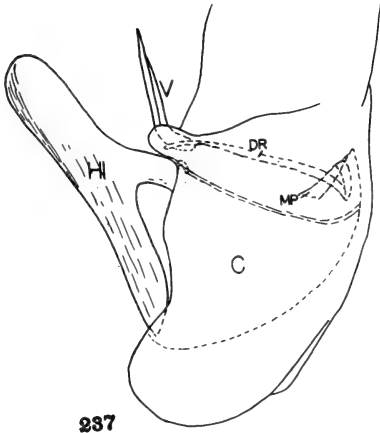
FIG. 247. Phallus, ventral view.

FIG. 248. Fifth sternite.

FIG. 249. Phallus, lateral view.

FIG. 250. Vesica, dorsal rods and median process, lateral view in natural relationship.

PLATE 17



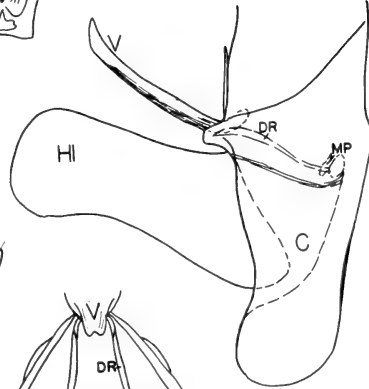
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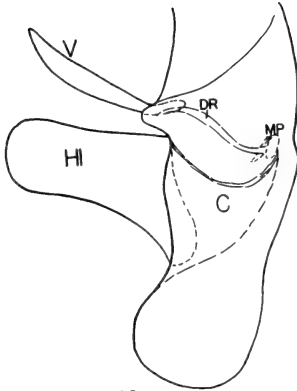
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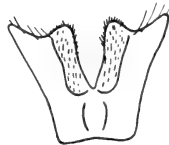
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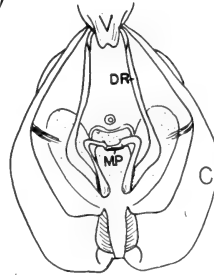
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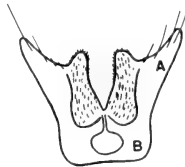
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242



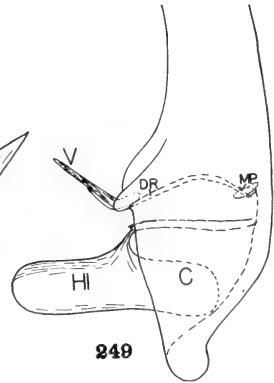
244



241



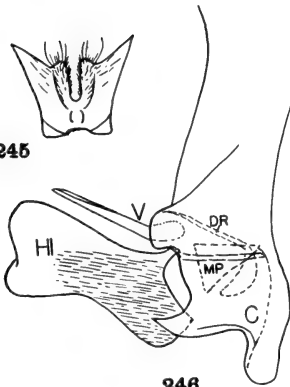
248



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245



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247



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PLATE 18

Ravinia pusiola (Van der Wulp)

- FIG. 251. Fifth sternite.
FIG. 252. Phallus, lateral view.
FIG. 253. Phallus, antero-ventral view—hillae removed.

Ravinia tancituro Roback

- FIG. 254. Fifth sternite.
FIG. 255. Phallus, lateral view.

Oxysarcodexia galeata (Aldrich)

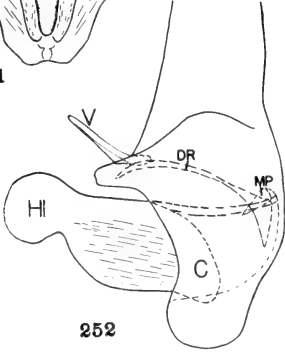
- FIG. 256. Fifth sternite.
FIG. 257. Phallus, lateral view.
FIG. 258. Median process and lateral filament, lateral view.
FIG. 259. Median process and lateral filaments, dorsal view.

Oxysarcodexia xanthosoma (Aldrich)

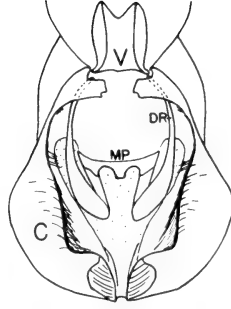
- FIG. 260. Tip of phallus, antero-dorsal view—vesica removed.
FIG. 261. Phallus, lateral view.



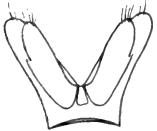
251



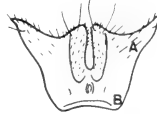
252



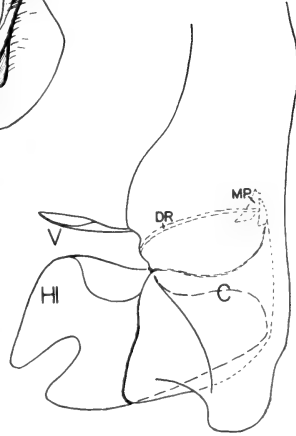
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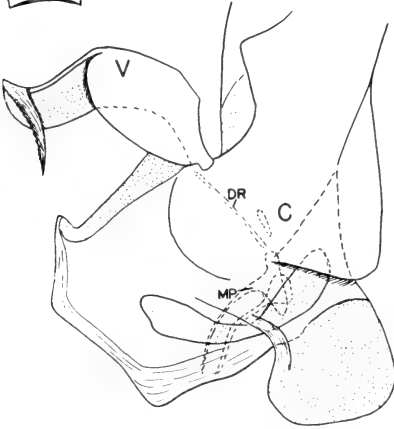
256



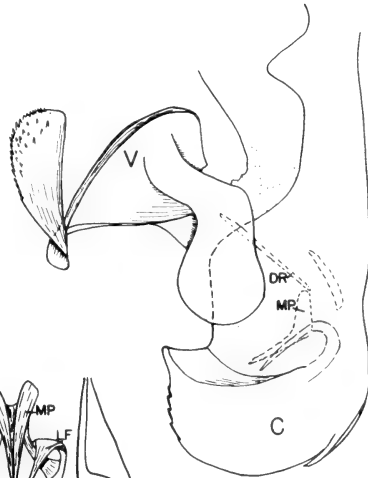
254



255



257



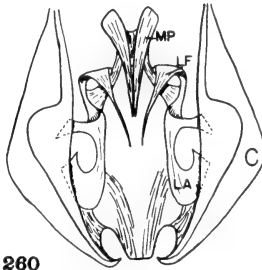
261



258



259



260

PLATE 19

Oxysarcodexia peltata (Aldrich)

FIG. 262. Phallus, lateral view.

FIG. 263. Fifth sternite.

Oxysarcodexia ochripyga (Van der Wulp)

FIG. 264. Phallus, lateral view.

FIG. 265. Fifth sternite.

FIG. 266. Median process, lateral filaments and arms, dorsal view.

FIG. 267. Median process and dorsal rods, lateral view.

Oxysarcodexia ventricosa (Van der Wulp)

FIG. 268. Lateral arm and filament, antero-meso-dorsal view—showing attachment of lateral arm to wall of corpus.

FIG. 269. Phallus, lateral view.

FIG. 270. Dorsal rods, median process, lateral arms and filaments, dorsal view.

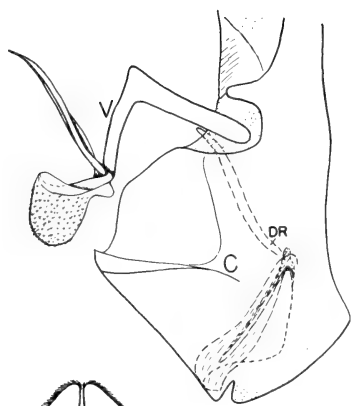
FIG. 271. Fifth sternite.

Oxysarcodexia trivialis (Van der Wulp)

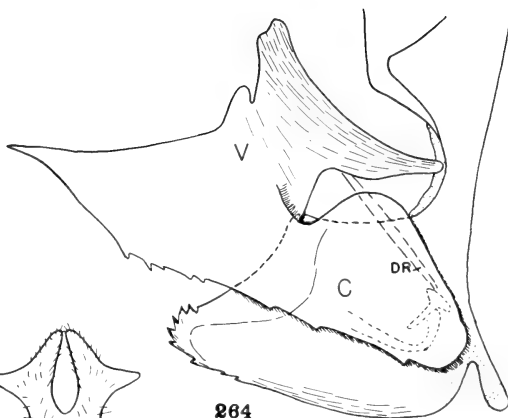
FIG. 272. Fifth sternite.

FIG. 273. Phallus, antero-ventral view.

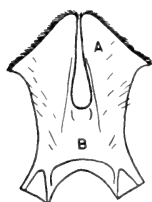
FIG. 274. Phallus, lateral view.



262



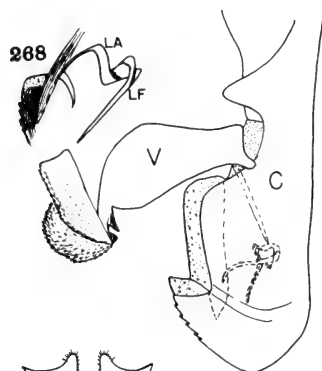
264



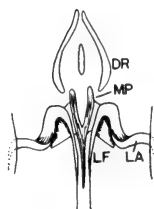
263



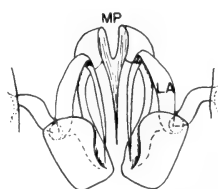
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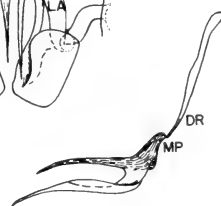
268



270



266

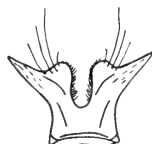


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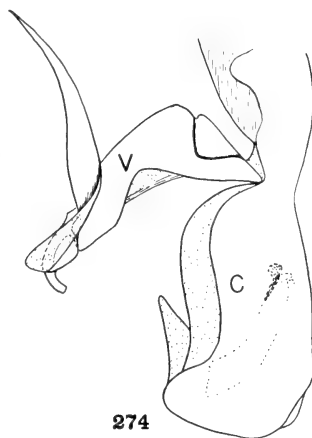
271



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273



274

PLATE 20

Oxysarcodexia cingarus (Aldrich)

FIG. 275. Fifth sternite.

FIG. 276. Phallus, lateral view.

FIG. 277. Median process and lateral filament, lateral view.

Oxysarcodexia bakeri (Aldrich)

FIG. 278. Median process, lateral filament and lateral arm, lateral view.

FIG. 279. Fifth sternite.

FIG. 280. Aedeagus, lateral view.

Hystericocnema plinthopyga (Wiedemann)

FIG. 281. Phallus, lateral view.

FIG. 282. Fifth sternite.

FIG. 283. Tip of phallus, antero-dorsal view.

FIG. 284. Left lateral filament, antero-ventral view.

Cistudinomyia cistudinis (Aldrich)

FIG. 285. Tip of phallus, antero-dorsal view—vesica removed.

FIG. 286. Phallus, lateral view.

FIG. 287. Fifth sternite.

Paraphrissopoda gulo (Fabricius)

FIG. 288. Fifth sternite.

FIG. 289. Phallus, lateral view.

PLATE 20

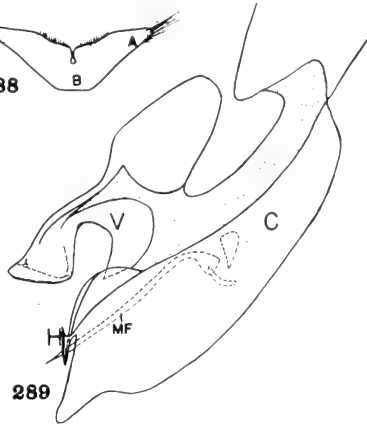
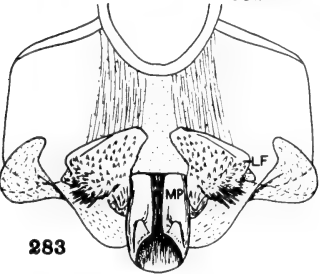
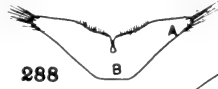
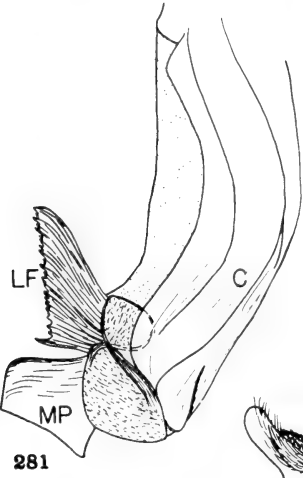
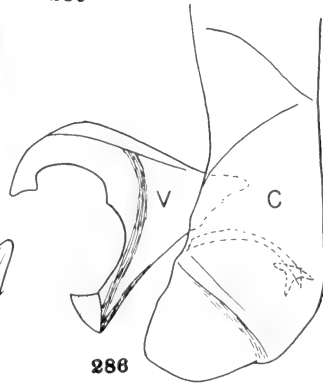
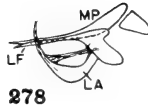
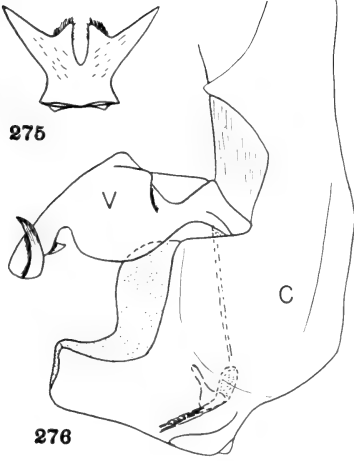


PLATE 21

Paraphrissopoda chrysostoma (Wiedemann)

FIG. 290. Phallus, lateral view.

FIG. 291. Vesica and harpes, dorsal view.

FIG. 292. Fifth sternite.

Paraphrissopoda capitata (Aldrich)

FIG. 293. Tip of phallus, antero-ventral view—vesica removed.

FIG. 294. Phallus, lateral view.

FIG. 295. Fifth sternite.

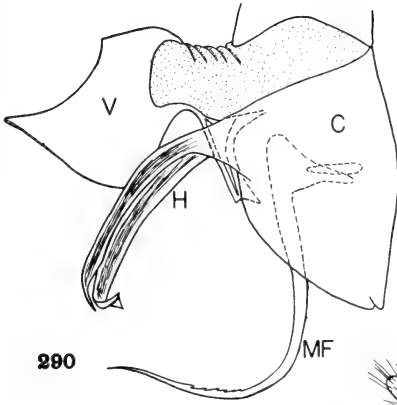
Paraphrissopoda amoena (Aldrich)

FIG. 296. Fifth sternite.

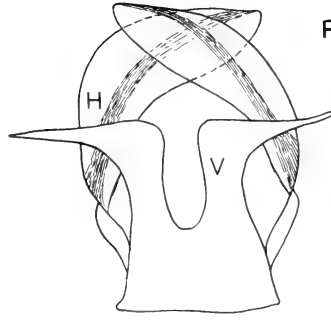
FIG. 297. Phallus, lateral view.

FIG. 298. Tip of phallus, antero-dorsal view—vesica removed.

PLATE 21



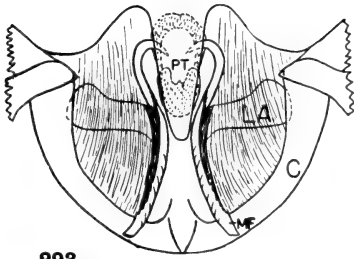
290



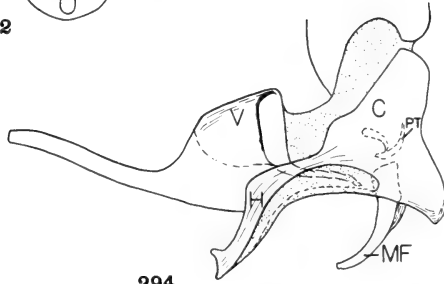
291



292



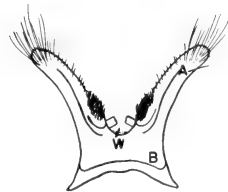
293



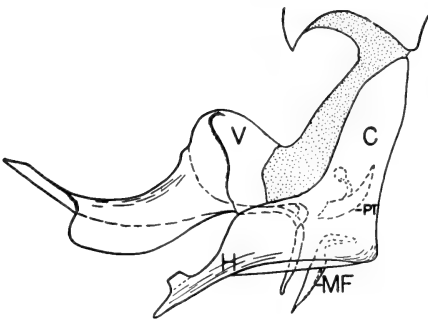
294



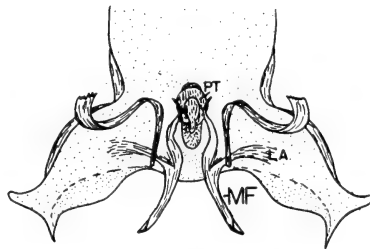
296



295



297



298

PLATE 22

Paraphrissopoda hillifera (Aldrich)

- FIG. 299. Phallus, lateral view.
FIG. 300. Phallus, antero-ventral view.
FIG. 301. Fifth sternite.

Sarcodexia lambens (Wiedemann)

- FIG. 302. Phallus, anterior view.
FIG. 303. Fifth sternite.
FIG. 304. Phallus, lateral view.

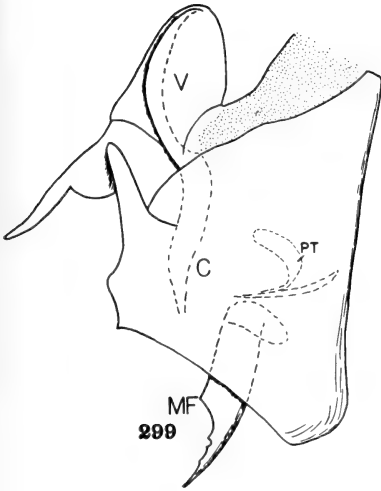
Euboettcheria australis Townsend

- FIG. 305. Base of phallus, anterior view.
FIG. 306. Fifth sternite.
FIG. 307. Phallus, lateral view.

Kellymyia kellyi (Aldrich)

- FIG. 308. Fifth sternite.
FIG. 309. Aedeagus, lateral view.

PLATE 22



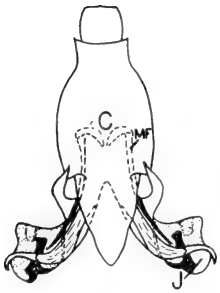
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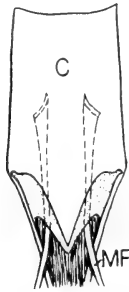
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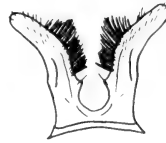
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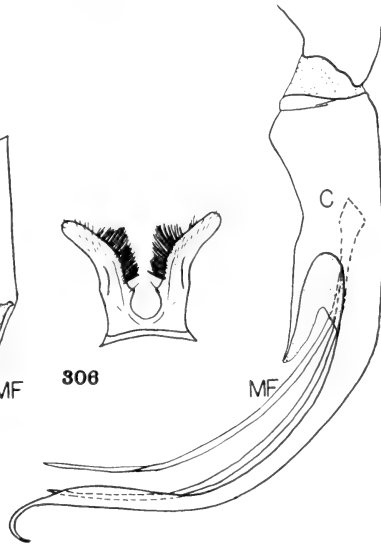
302



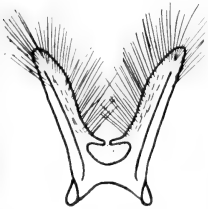
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306



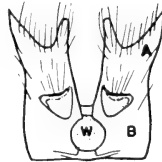
307



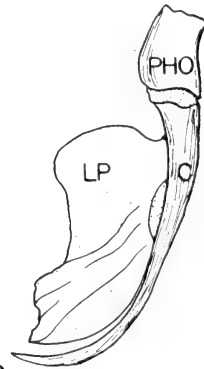
303



304



308



309

PLATE 23

Rafaelia rufiventris Townsend

FIG. 310. Phallus, lateral view.

FIG. 311. Phallus, anterior view.

FIG. 312. Fifth sternite.

Rafaelia ampulla (Aldrich)

FIG. 313. Phallus, lateral view.

FIG. 314. Tip of phallus, antero-dorsal view.

FIG. 315. Fifth sternite, dotted section missing in specimen.

Metoposarcophaga (Zygastropyga) sulculata (Aldrich)

FIG. 316. Aedeagus, lateral view.

FIG. 317. Phallus, ventral view.

FIG. 318. Median process, lateral view.

FIG. 319. Median process and lateral filaments, dorsal view.

FIG. 320. Fifth sternite.

Metoposarcophaga (Metoposarcophaga) importuna (Walker)

FIG. 321. Fifth sternite.

FIG. 322. Median process, lateral view.

FIG. 323. Lateral filament, lateral view.

FIG. 324. Aedeagus, lateral view.

Metoposarcophaga (Zygastropyga) villipes (Van der Wulp)

FIG. 325. Fifth sternite.

FIG. 326. Aedeagus, lateral view.

PLATE 23

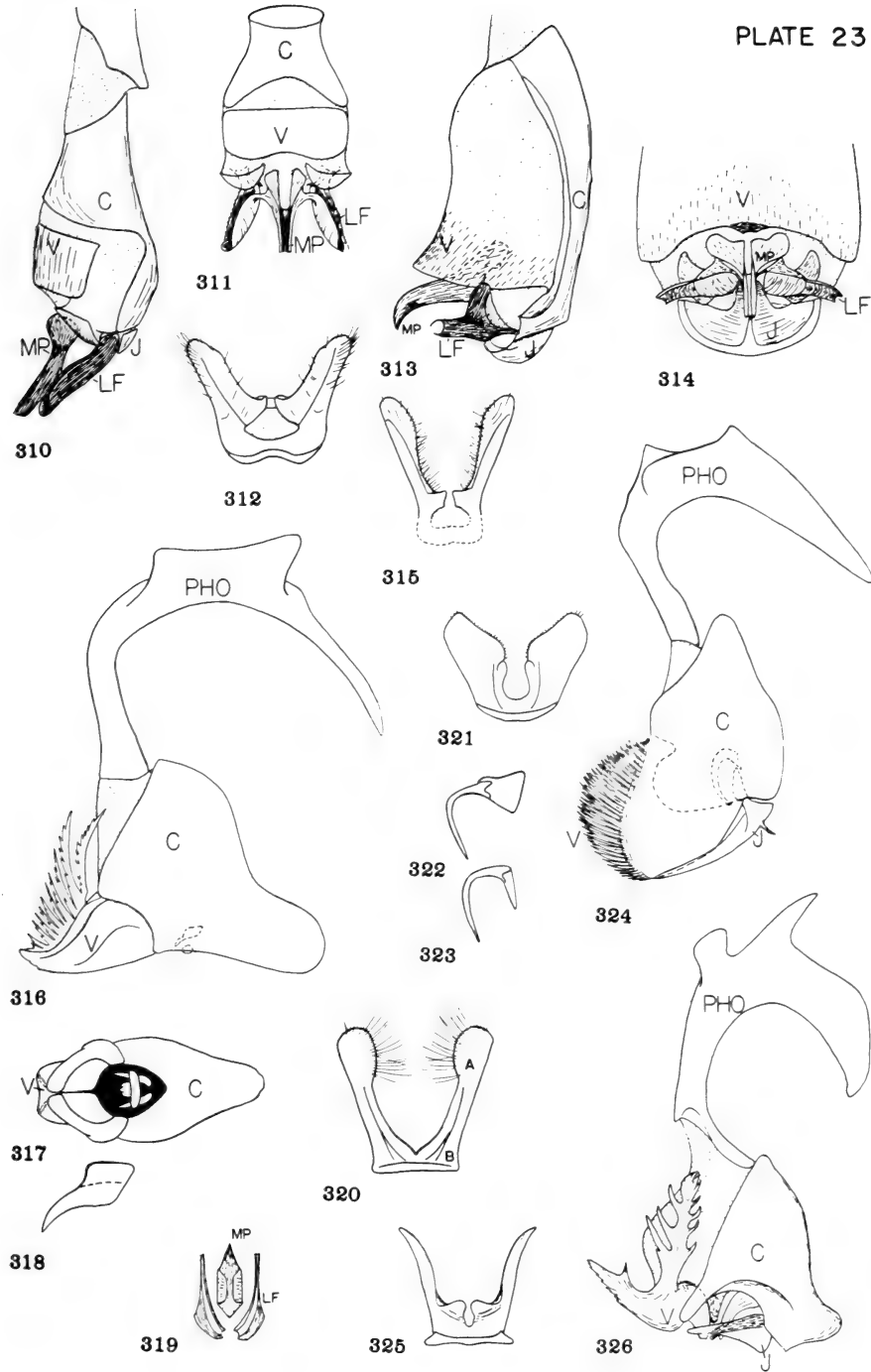


PLATE 24

Metoposarcophaga (Zygastropyga) aurea (Townsend)

FIG. 327. Aedeagus, lateral view.

FIG. 328. Fifth sternite.

FIG. 329. Phallus, ventral view.

Aphelomyia welchi (Hall)

FIG. 330. Phallus, lateral view.

FIG. 331. Phallus, antero-ventral view.

FIG. 332. Fifth sternite.

Metoposarcophaga (Zygastropyga) cantenea (Roback)

FIG. 333. Genitalia, lateral view.

FIG. 334. Anal plates and forceps, caudal view.

FIG. 335. Aedeagus, lateral view.

FIG. 336. Phallus, ventral view.

PLATE 24

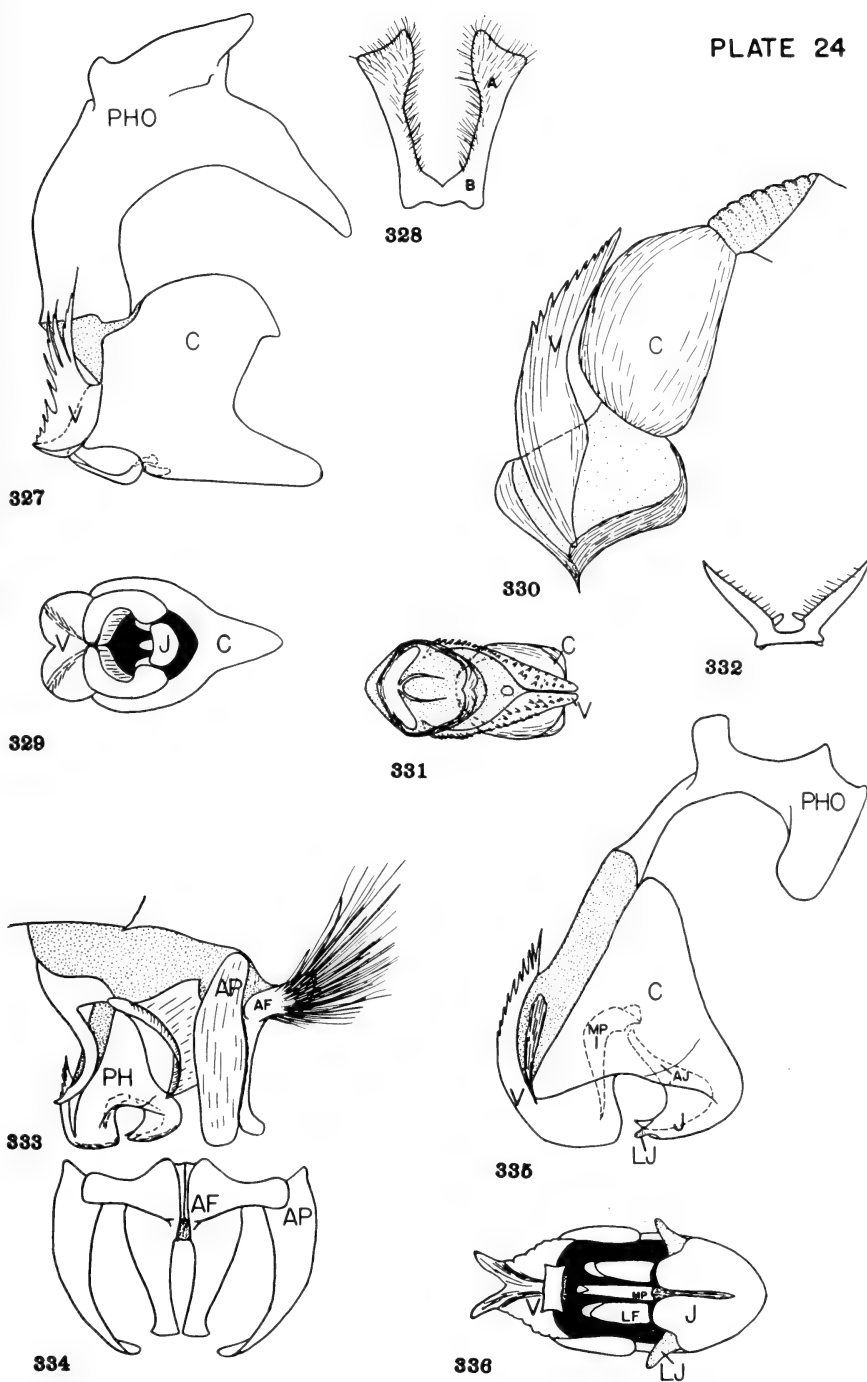


PLATE 25

Boettcheria cimbicis (Townsend)

FIG. 337. Phallus, lateral view.

FIG. 338. Fifth sternite.

FIG. 339. Vesica, anterior view—membranous parts removed.

FIG. 340. Juxta and median process, lateral view.

Boettcheria bisetosa Parker

FIG. 341. Phallus, lateral view.

FIG. 342. Juxta, anterior juxtal process and median process, lateral view.

FIG. 343. Right lateral filament, lateral view.

Boettcheria carata Roback

FIG. 344. Fifth sternite.

FIG. 345. Phallus, lateral view.

Boettcheria latisterna Parker

FIG. 346. Phallus, lateral view.

FIG. 347. Fifth sternite.

FIG. 348. Vesica, anterior view.

FIG. 349. Juxta, anterior juxtal process and median process, lateral view.

PLATE 25

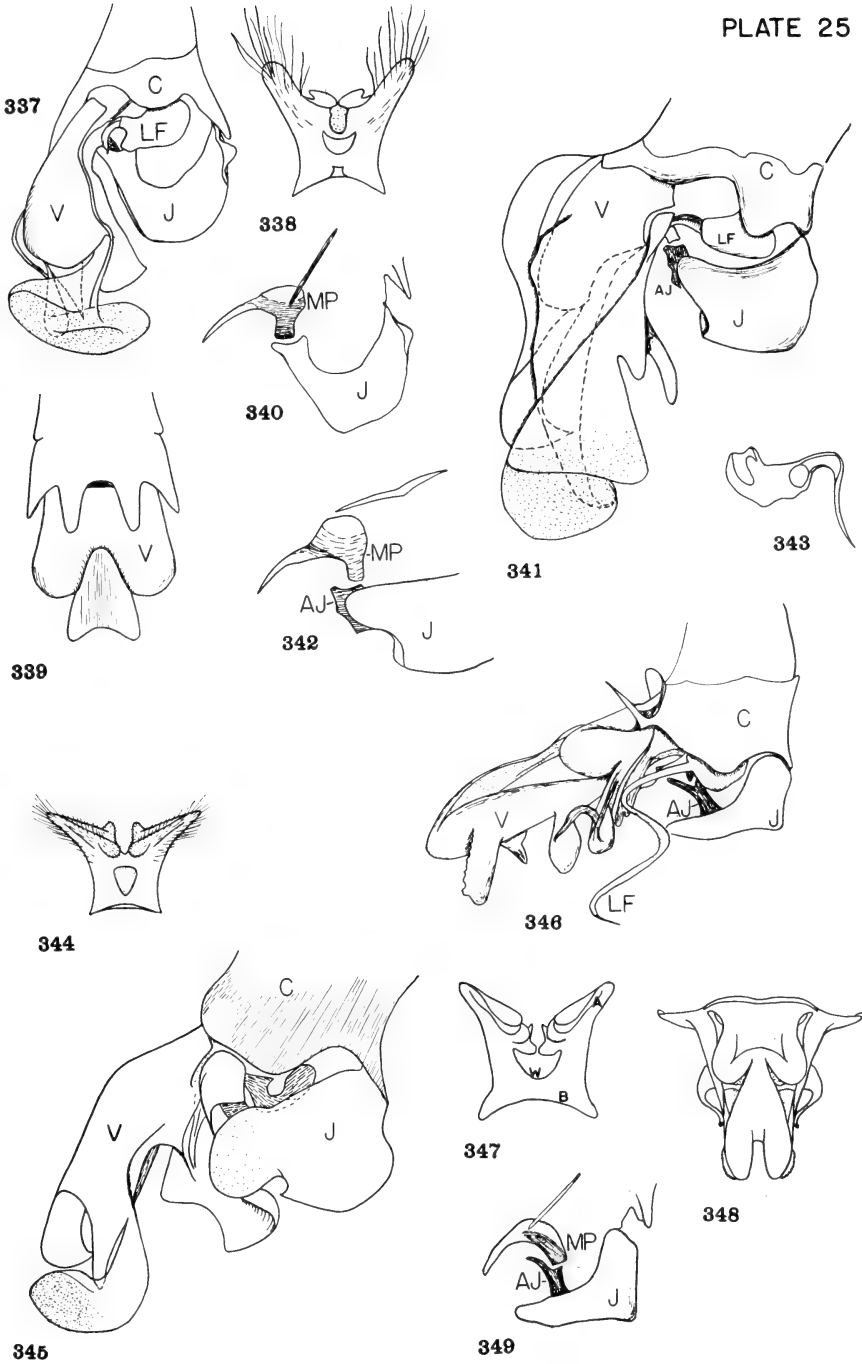


PLATE 26

Spirobolomyia pallipes (Walker)

FIG. 350. Phallus, lateral view—left lateral plate removed.

FIG. 351. Fifth sternite.

Spirobolomyia flavipes (Aldrich)

FIG. 352. Phallus, lateral view.

FIG. 353. Corpus, caudal view.

FIG. 354. Fifth sternite.

FIG. 355. Lateral filaments, median process and juxta, lateral view in natural relationship.

Cucullomyia texana (Aldrich)

FIG. 356. Fifth sternite.

FIG. 357. Phallus, lateral view.

FIG. 358. Juxta and base of median process, lateral view.

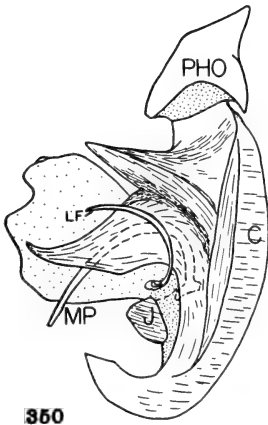
FIG. 359. Phallus, antero-dorsal view.

Spirobolomyia basalis (Walker)

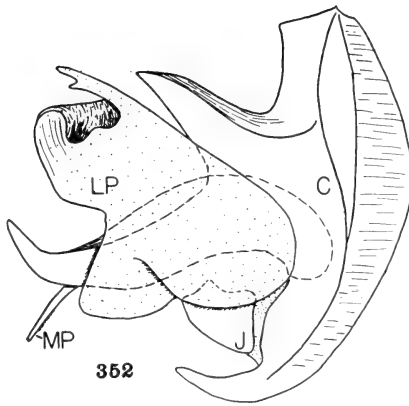
FIG. 360. Phallus, lateral view.

FIG. 361. Fifth sternite.

PLATE 26



350



352



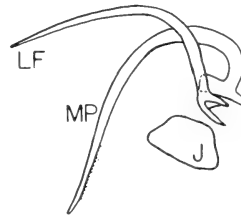
353



351



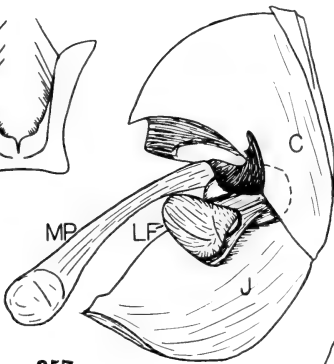
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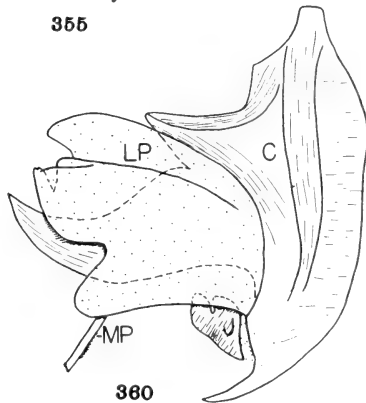
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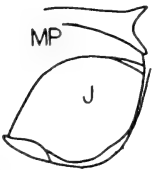
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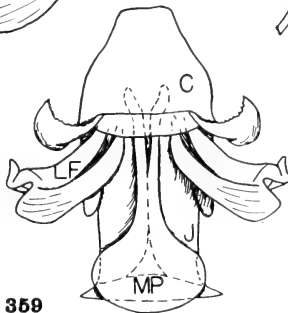
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361

PLATE 27

Tylomyia pedunculata (Hall)

FIG. 362. Phallus, lateral view.

FIG. 363. Phallus, antero-ventral view.

FIG. 364. Lateral filaments, median process and juxta, ventral view.

FIG. 365. Fifth sternite.

Fletcherimyia fletcheri (Aldrich)

FIG. 366. Phallus, anterior view.

FIG. 367. Phallus, lateral view.

FIG. 368. Stemmatis and juxta, lateral view.

FIG. 369. Fifth sternite.

Fletcherimyia jonesi (Aldrich)

FIG. 370. Stemmatis, antero-dorsal view.

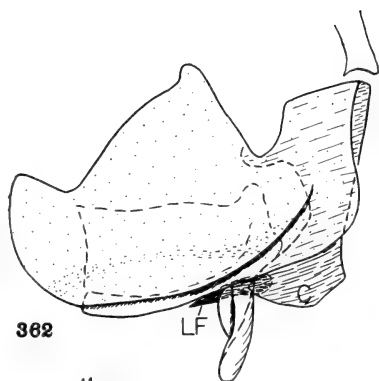
FIG. 371. Fifth sternite.

FIG. 372. Phallus, lateral view.

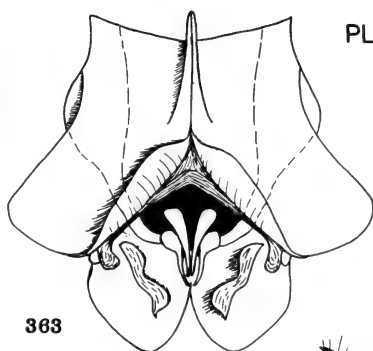
Fletcherimyia rileyi (Aldrich)

FIG. 373. Fifth sternite.

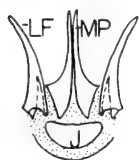
FIG. 374. Phallus, lateral view.



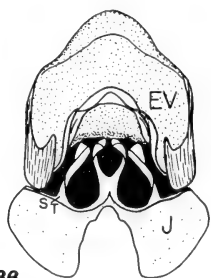
362



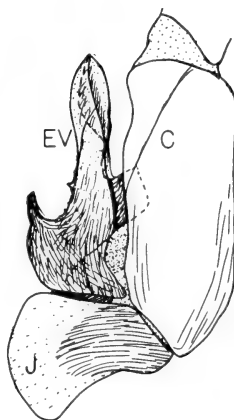
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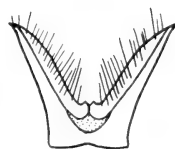
364



366



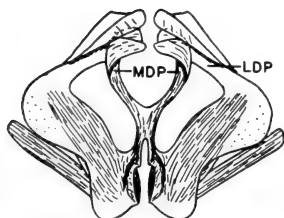
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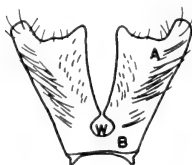
365



368



370



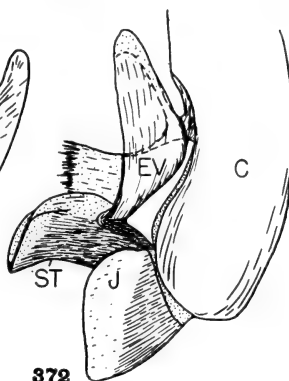
373



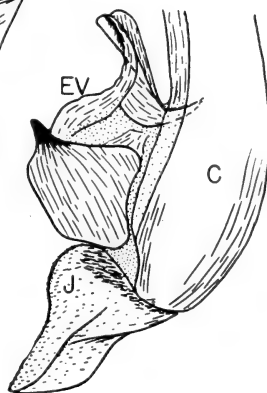
369



371



372



374

PLATE 28

Fletcherimyia celarata (Aldrich)

FIG. 375. Phallus, lateral view.

FIG. 376. Stemmatis, antero-dorsal view.

Servaisia (*Protodexia*) *opifera* (Coquillett)

FIG. 377. Phallus, lateral view.

FIG. 378. Phallus, antero-dorsal view.

FIG. 379. Fifth sternite.

Servaisia (*Protodexia*) *hunteri* (Hough)

FIG. 380. Phallus, lateral view.

FIG. 381. Fifth sternite.

FIG. 382. Tip of phallus, antero-ventral view.

Servaisia (*Servaisia*) *coloradensis* (Aldrich)

FIG. 383. Phallus, lateral view.

FIG. 384. Phallus, anterior view.

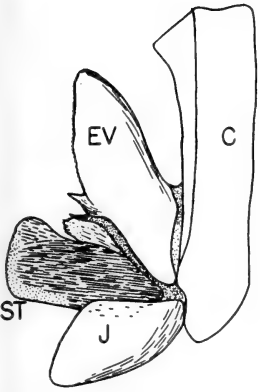
Servaisia (*Servaisia*) *erythrura* (Meigen)

FIG. 385. Tip of phallus, antero-dorsal view.

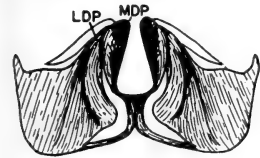
FIG. 386. Phallus, lateral view.

FIG. 387. Fifth sternite, dotted part missing in specimen.

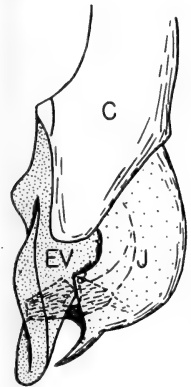
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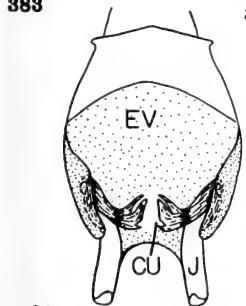
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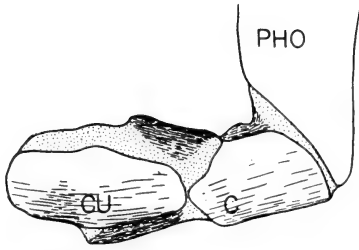
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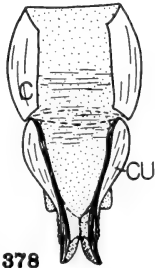
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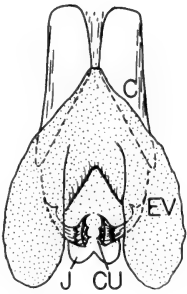
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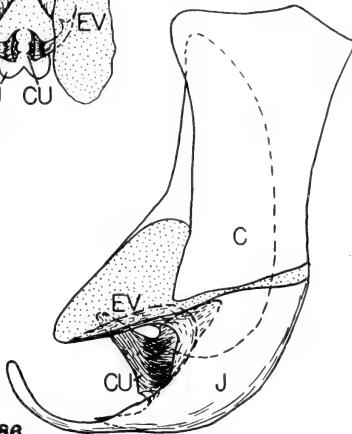
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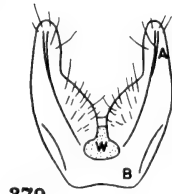


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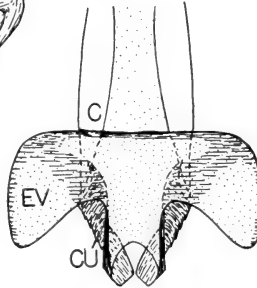
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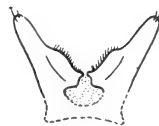
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PLATE 29

Servaisia (Sarpedia) setigera (Aldrich)

FIG. 388. Fifth sternite.

FIG. 389. Phallus, lateral view.

FIG. 390. Phallus, anterior view.

Servaisia (Servaisia) uncata (Van der Wulp)

FIG. 391. Fifth sternite.

FIG. 392. Phallus, anterior view.

FIG. 393. Phallus, lateral view.

Servaisia (Servaisia) falciformis (Aldrich)

FIG. 394. Fifth sternite.

FIG. 395. Phallus, lateral view.

FIG. 396. Phallus, anterior view.

Servaisia (Acridophaga) aculeata (Aldrich)

FIG. 397. Phallus, lateral view.

FIG. 398. Phallus, anterior view.

Servaisia (Acridophaga) reversa (Aldrich)

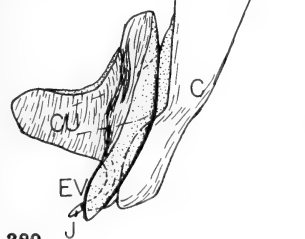
FIG. 399. Phallus, lateral view.

FIG. 400. Fifth sternite.

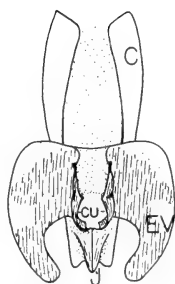
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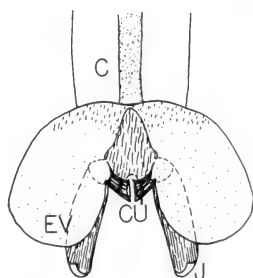
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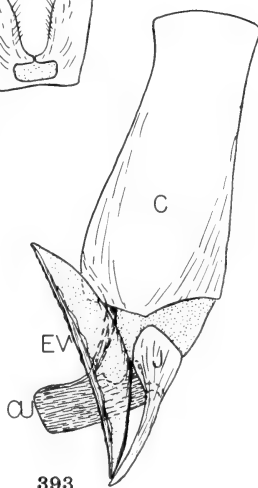
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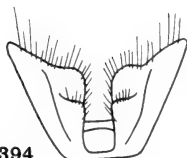
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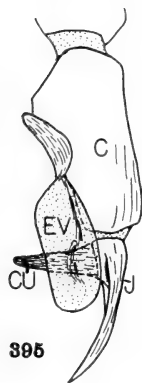
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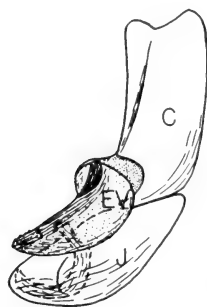
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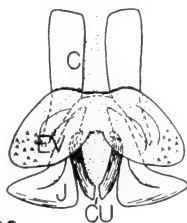
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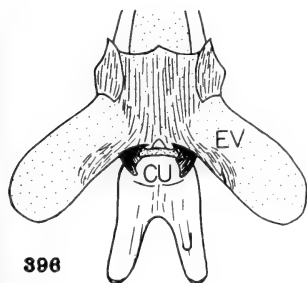
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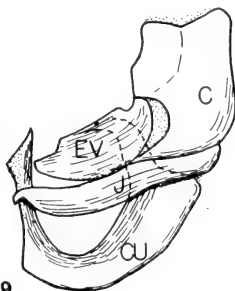
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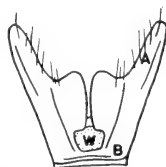
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PLATE 30

Servaisia (Acridophaga) angustifrons (Aldrich)

- FIG. 401. Phallus, lateral view.
FIG. 402. Phallus, anterior view.
FIG. 403. Phallus, caudal view.
FIG. 404. Fifth sternite.

Servaisia (Acridophaga) caridei (Brèthes)

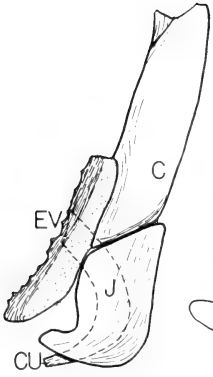
- FIG. 405. Fifth sternite.
FIG. 406. Phallus, anterior view.
FIG. 407. Phallus, lateral view.

Kurtomyia postilla (Reinhard)

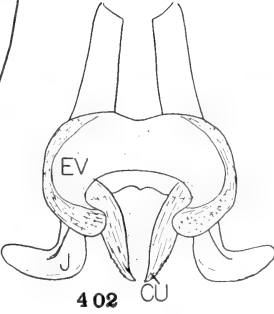
- FIG. 408. Fifth sternite.
FIG. 409. Phallus, anterior view.
FIG. 410. Phallus, lateral view.

Servaisia (Speciosia) speciosa (Lopes)

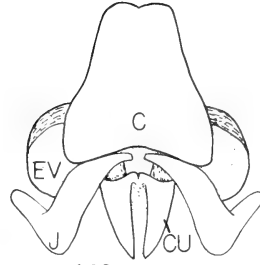
- FIG. 411. Fifth sternite.
FIG. 412. Phallus, lateral view.



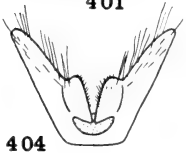
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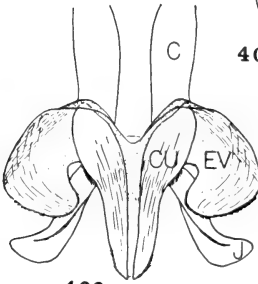
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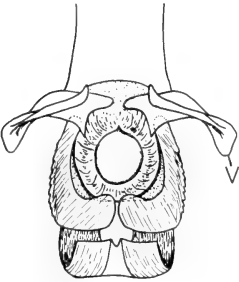
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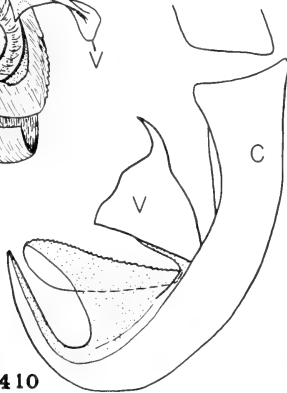
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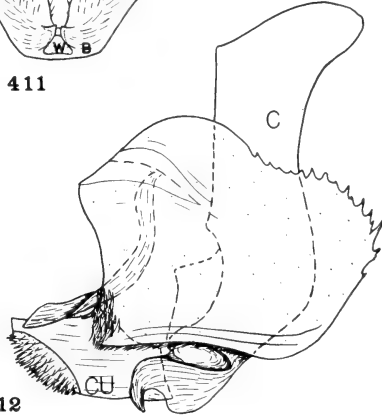
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PLATE 31

Acandotheca (Stenolaucotheca) spatulata (Aldrich)

FIG. 413. Fifth sternite.

FIG. 414. Phallus, lateral view.

FIG. 415. Phallus, anterior view.

Acandotheca (Tephromyiella) atlanis (Aldrich)

FIG. 416. Phallus, lateral view.

FIG. 417. Fifth sternite.

FIG. 418. Tip of phallus, antero-ventral view.

Acandotheca (Mecynocorpus) salva (Aldrich)

FIG. 419. Fifth sternite.

FIG. 420. Phallus, lateral view.

FIG. 421. Limen, dorsal view.

Acandotheca (Lepyria) melampyga (Aldrich)

FIG. 422. Fifth sternite.

FIG. 423. Phallus, lateral view.

FIG. 424. Phallus, anterior view.

Acandotheca (Acandotheca) alcedo (Aldrich)

FIG. 425. Tip of phallus, anterior view.

FIG. 426. Fifth sternite.

FIG. 427. Phallus, lateral view.

PLATE 31

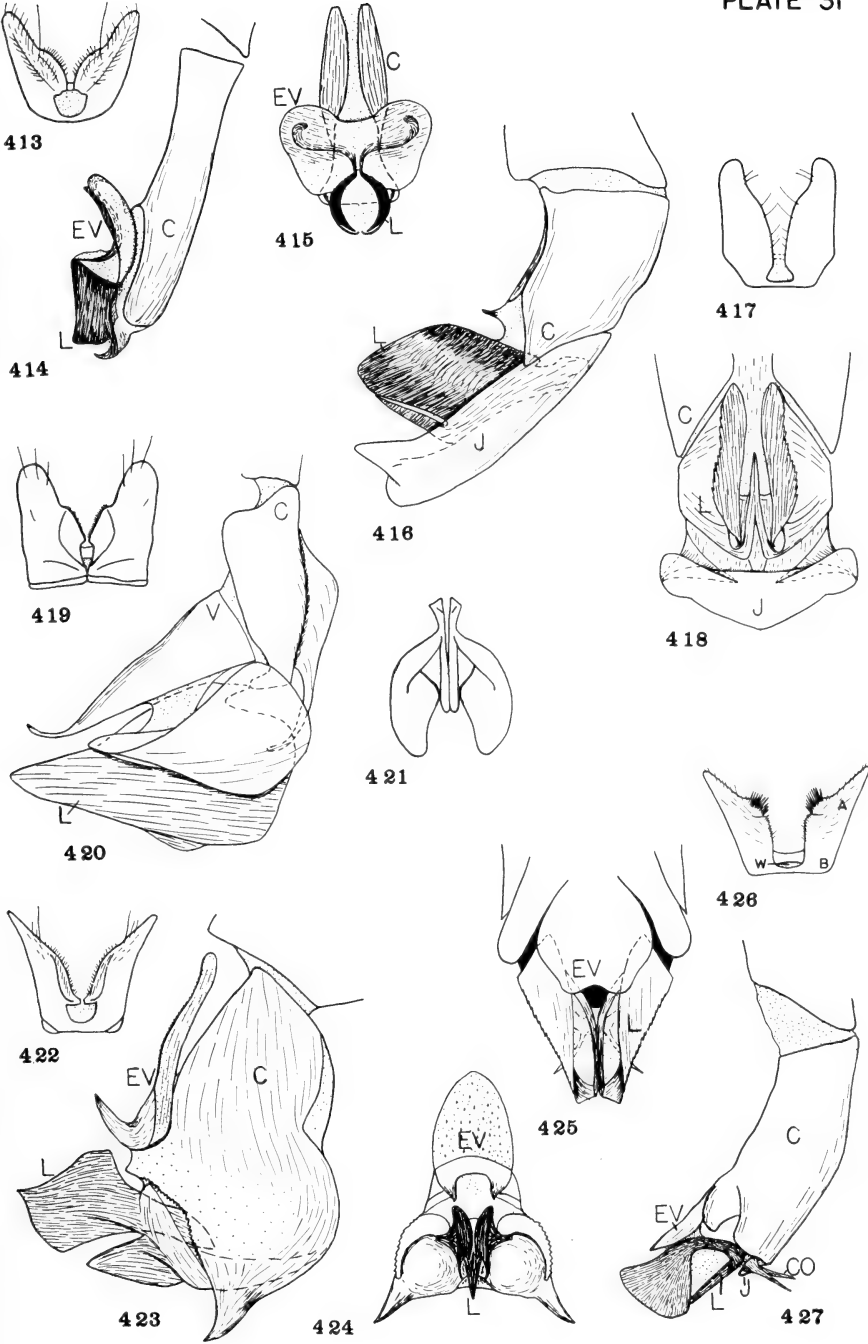


PLATE 32

Acandotheca (Acandotheca) hamata (Aldrich)

FIG. 428. Phallus, lateral view.

FIG. 429. Phallus, antero-dorsal view.

FIG. 430. Fifth sternite.

Acandotheca (Acandotheca) rudis (Aldrich)

FIG. 431. Fifth sternite.

FIG. 432. Phallus, lateral view.

FIG. 433. Phallus, ventro-caudal view.

Acandotheca (Acandotheca) masculina (Aldrich)

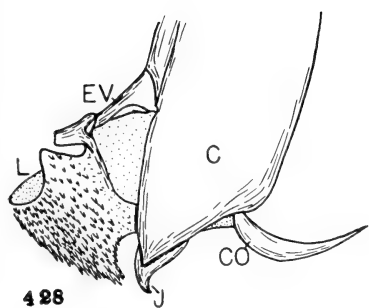
FIG. 434. Phallus, anterior view.

FIG. 435. Phallus, lateral view.

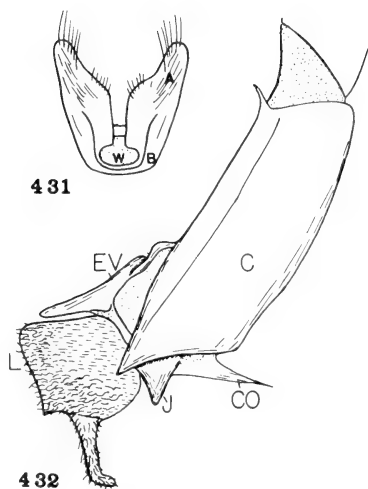
Acandotheca (Acandotheca) prohibita (Aldrich)

FIG. 436. Phallus, lateral view.

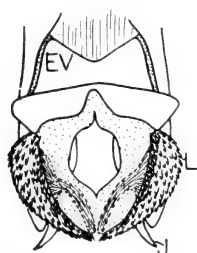
PLATE 32



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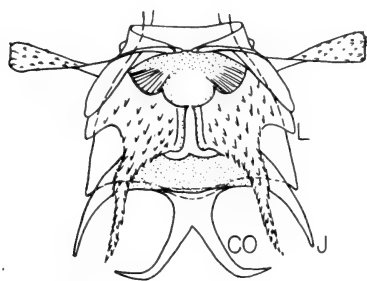
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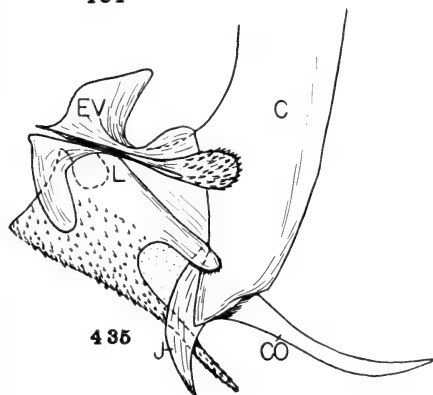
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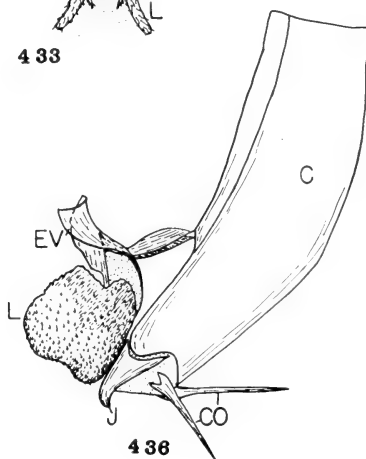
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PLATE 33

Acandotheca (Acandotheca) complosa (Reinhard)

FIG. 437. Phallus, lateral view.

FIG. 438. Phallus, anterior view.

FIG. 439. Fifth sternite.

Acandotheca (Acandotheca) eleodis (Aldrich)

FIG. 440. Fifth sternite.

FIG. 441. Phallus, lateral view.

Xenoppia hypopygialis Townsend

FIG. 442. Phallus, anterior view—lateral plates spread apart.

FIG. 443. Phallus, lateral view.

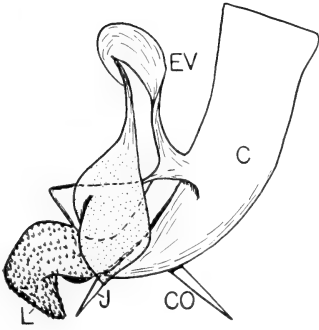
FIG. 444. Tip of phallus, lateral view—lateral plates removed.

FIG. 445. Fifth sternite.

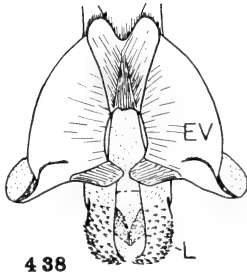
Neophyto setosa Coquillett

FIG. 446. Phallus, lateral view.

FIG. 447. Fifth sternite.



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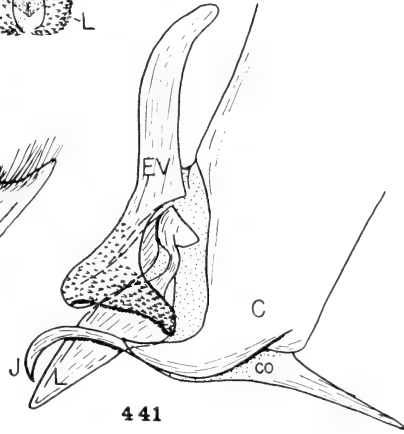
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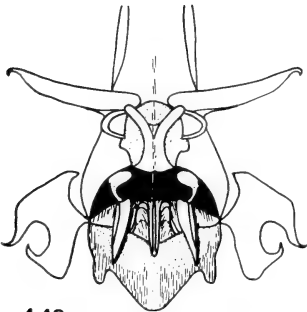
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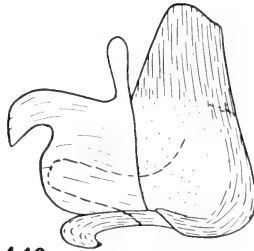
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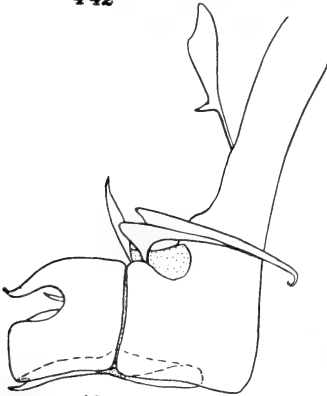
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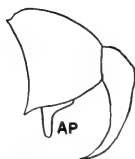
PLATE 34

- FIG. 448. *Wohlfahrtia meigeni* (Schiner), abdomen, dorsal view. (After Aldrich 1916.)
- FIG. 449. *Sarcofahrtia ravinia* Parker, anal plate and anal forceps, lateral view. (After Aldrich 1916.)
- FIG. 450. *Boettcheria similis* Lopes, anal plate. (After Lopes 1946a.)
- FIG. 451. *Imparia impar* (Aldrich), tip of anal forceps, lateral view. (After Aldrich 1916.)
- FIG. 452. *Kellymyia kellyi* (Aldrich), tip of anal forceps, lateral view. (After Aldrich 1916.)
- FIG. 453. *Hystericocnema plinthopyga* (Wiedemann), anal forceps, lateral view. (After Aldrich 1916.)
- FIG. 454. *Tylomyia texana* (Aldrich), anal forceps, lateral view. (After Aldrich 1916.)
- FIG. 455. *Argoravinia modesta* (Wiedemann), anal forceps, lateral view. (After Aldrich 1916.)
- FIG. 456. *Acandotheca* (*Acandotheca*) *eleodis* (Aldrich), anal forceps, lateral view. (After Aldrich 1916.)
- FIG. 457. *Acandotheca* (*Mecynocorpus*) *salva* (Aldrich), tip of anal forceps, lateral view. (After Aldrich 1916.)
- FIG. 458. *Servaisia* (*Speciosia*) *speciosa* (Lopes), anal forceps, lateral view. (After Lopes 1946a.)
- FIG. 459. *Wohlfahrtiopsis johnsoni* (Aldrich), tip of anal forceps, lateral view. (After Aldrich 1916.)
- FIG. 460. *Metoposarcophaga* (*Zygastropyga*) *sulculata* (Aldrich), apical section of abdomen, lateral view. (After Aldrich 1916.)

PLATE 34



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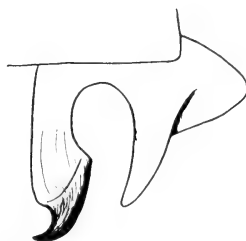
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X. Index

The page entries in **boldface** refer to the main treatment of the subgenera, genera, and higher categories. Names that are synonyms or of changed generic placement are in *italics*. Those names which are in keys or in figure headings are not listed.

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